EVOLUTION OF VARIATION IN PLUMAGE AND ORNAMENTATION IN LEAST AUKLETS *Aethia pusilla* (PALLAS)

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Evolution of Variation in Plumage and Ornamentation in Least Auklets *Aethia pusilla* (Pallas)

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ABSTRACT

Conspicuous ornaments with little apparent cost are ubiquitous in nature, but their function and evolutionary origins are poorly understood. Most evolutionary models predict that ornament expression is associated with a cost and correlated with individual quality. I investigated ornamentation in the Least Auklet (*Aethia pusilla*), a seabird that displays multiple ornaments and a highly variable degree of ventral mottling. Phylogenetic reconstruction showed that the ancestral state is likely ventrally white for most seabird clades, but only mostly white in auklets. I measured several novel indicators of quality, including measures of take-off performance, and their relations to plumage and ornamentation. Power and acceleration, 0.17 s after take-off were the most repeatable measures (repeatability = 75 % and 72 %, respectively). AIC-based model selection revealed significant interactions in the relationships of two low-cost ornaments (bill knob and auricular plume) with indicators of individual quality (hematocrit, leucocrit, mass/condition, and take-off acceleration). Mass was positively related to both bill knob and auricular plume size in subadults but not in adults, and inversely related to ventral plumage mottling in adults but not in subadults. I rejected the individual recognition hypothesis, which predicts a deviation from a multivariate normal distribution of ornaments that was not found in this study. The birds with less mottling are more conspicuous on land where predation is a constant threat. Predation by Glaucous-winged Gulls (*Larus glaucescens*) could be a vulerability handicap that ensures the reliability of the plumage as a social signal. Gulls attacked experimentally-whitened model auklets significantly less often than darkened models (P = 0.036), as predicted if mottling is

dependent on physical fitness and acts as a signal of escape potential. Also in accordance with prediction, auklets on a different island without aerial predators had significantly lighter plumage ($P < 0.001$), suggesting a lower cost to conspicuousness in the absence of aerial predators. I did not observe a correlation between take-off acceleration and plumage mottledness, however. My results suggest that ornaments are related to condition in subadults, and that plumage functions as a vulnerability handicap in interactions with gulls.

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While working on penguins in New Zealand it occurred to me that the ornaments of crested penguins must have evolved through mutual sexual selection. My supervisor Lloyd Davis recommended I look up some of Ian Jones's work; we subsequently met in South Africa and that's how a German ended up going to school in Newfoundland studying auklets in Alaska.

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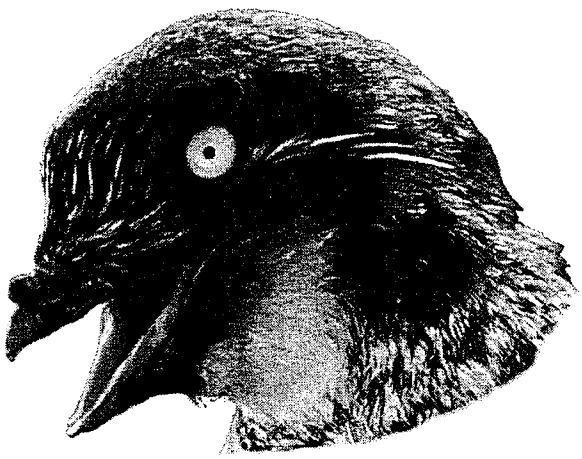
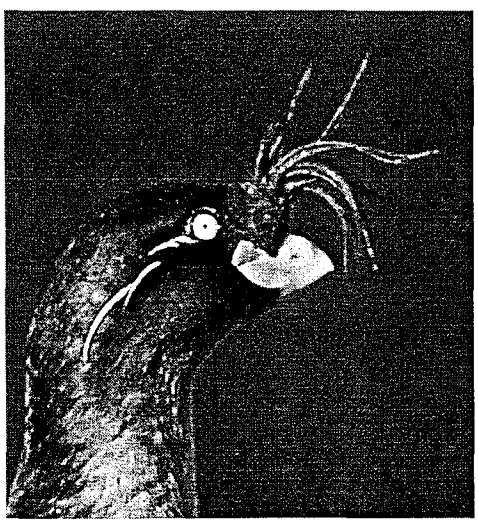
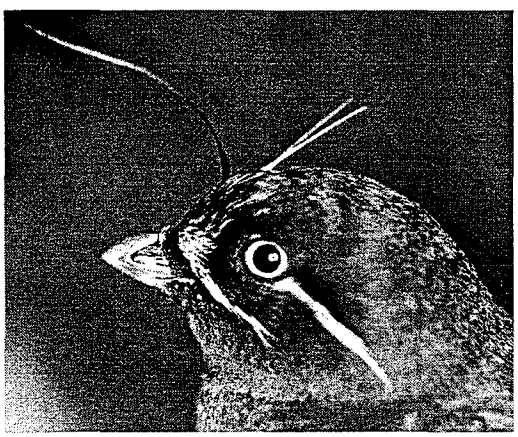
LIST OF ABBREVIATIONS AND SYMBOLS

β	parameter in a linear model
ε	error term in a linear model
χ^2	chi-square statistic
ACWERN	Atlantic Cooperative Wildlife Ecology Research Network
AIC	Akaike's An Information Criterion
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
CV	coefficient of variation
df	degrees of freedom
F	F statistic
HAST	Hawaii-Aleutian Standard Time
MANOVA	Multivariate Analysis of Variance
N	sample size
NSERC	Natural Sciences and Engineering Research Council of Canada
NWR	National Wildlife Refuge
PCA	Principal Component Analysis
r	repeatability; also Pearson's correlation coefficient
SD	standard deviation
SE	standard error
t	t statistic

Chapter 1.
Introduction and Overview







Conspicuousness in nature

Getting noticed is essential to many aspects of life. A look into a 19th century curiosity-cabinet filled with hundreds of exotic butterflies and birds might suggest that life is not a struggle for survival but rather a struggle to be seen. Why is it so important to get noticed? If life is a struggle for survival, should not all but the top predators be cryptic to avoid detection? Increased predation is not the only cost associated with conspicuousness; some displays are energy intensive (e.g. display flights, long tails).

Here I define conspicuousness as any trait that is used to attract notice to its bearer. Since it is possible to attract attention over every sensory mechanism available, conspicuousness will necessarily include optical, behavioural, acoustical, structural (shape), and chemical traits – potentially also exotics such as electrical fields (electrical fish) and thermal radiation (arctic flowers acting as solar collectors to attract pollinators). It follows that the opposite of conspicuousness is crypsis and that the evolution of both concepts should be treated within one unified theoretical framework.

My definition means that some traits will be conspicuous to conspecifics or predators, even though they appear cryptic to human beings. For example, elephants (*Elephas maximus* and *Loxodonta africana*) appear silent to humans most of the time but transmit infrasound, audible to other elephants over several kilometres (Payne *et al.* 1986; Poole *et al.* 1988). Similarly, Blue Tits (*Parus caeruleus*) and Zebra Finches (*Taeniopygia guttata*) are strikingly sexually dimorphic in the UV spectrum and have been shown to base their mate-choice on the extent of these UV-reflective colourations

(Bennett *et al.* 1996; Andersson *et al.* 1998). Bats (Microchiroptera) or electric fish (e.g. *Malapterus electricus*) will obviously have their very own perception of conspicuousness. I will exclude from this treatment plants, fungi and unicellular organisms as receptors because of their lack of a nervous system and therefore rather limited behaviour. On the other hand, brightly coloured coral fish may appear much less conspicuous in front of their natural brightly-coloured background (Barry, and Hawryshyn 1999). Background is important because *contrasts* are the essence of any conspicuousness (Endler 1990). Two types of contrasts can be distinguished: contrasts with the background, and contrasting patterns on the individual itself ("inherent"). Which of the two is more important depends on the observer's perspective. "Close quarter conspicuousness" relies on inherent contrasts and is independent of the background, while "long-distance conspicuousness" or "detectability" takes the organism's natural environment into account (Guilford, and Dawkins 1991; Götmark, and Unger 1994). At least for organisms capable of higher cognitive processes, anything deviating from their habits will appear as conspicuous as well. This could be an unusual behaviour, or aberrations in pigmentation such as albinism or melanism, or vocalisation. Typically, close-quarter conspicuousness is more relevant to sexual selection, while long-range conspicuousness results in a prey being detected by a predator.

Sexual selection leading to conspicuousness

Darwin (1871) explained the elaborate ornaments of the peacock's tail, which were in apparent contradiction to the theory of natural selection, with sexual selection. If females have a preference for males with long tails, then long-tailed males will evolve as

a result of female choice, even if such a tail does not provide a survival benefit by itself. Darwin did not explain, however, why females should prefer males with conspicuous ornaments.

Fisherian runaway process

The Fisherian runaway process (Fisher 1915, 1930) was the first attempt to explain the evolution of female preference. The idea is that the more choosy sex (usually females) has a preference for a heritable trait, which is then passed on to their sons. Once started, a chain-reaction is set off which should lead to the rapid evolution of conspicuous traits that are of no apparent function other than producing 'sexy' sons. In this scenario the females can evolve a preference for super-males, while the males might reach their physiological limits for that particular trait. Although runaway process has the potential to aid many evolutionary mechanisms, it is unclear how the initial female preference evolves.

Honest signal

In mate choice two factors will influence the chooser's fitness: the genetic make-up ("good genes" as well as compatible genes resulting in a good mix), and current condition of the partner, the latter being important for parental provisioning and social status. If partners base their decision on signals of quality received from each other, these signals will have to be honest to be evolutionarily stable (Johnstone, and Grafen 1992). Honesty can be achieved through a 'strategic handicap' (Zahavi 1975; Anderson 1982) in which an associated cost prevents cheating. The cost should be designed in a way that it takes away from the trait that is being advertised, e.g. to advertise physical strength the signal

itself has to reduce strength. "The cost of a signal is a key to its meaning" (Grafen 1990, p. 534). If it is costly to an animal's health to be conspicuous, e.g., if the immune system is weakened, then conspicuousness could evolve as an honest signal for health.

Speciation

Speciation by reinforcement is a theoretical mechanism whereby two geographically separated and partly differentiated populations come into secondary contact. Differentiation between the two populations will lead to decreased fitness of hybrids creating a hybrid-sink. The hybrid sink leads to selection for isolation mechanisms (Dobzhansky 1937). Conspicuous, ornamental traits could thereby evolve to help separate the two populations and avoid further hybridisation. Although intuitively convincing, the possibility of such a mechanism has been challenged in simulation studies, which showed that the rarer form becomes extinct in the hybrid-sink before isolation mechanisms could evolve (Paterson 1985; Spencer *et al.* 1986). Nevertheless, a recent study claims evidence that speciation by reinforcement was observed in the Pied Flycatcher (*Ficedula hypoleuca*) in central Europe (Sætre *et al.* 1997). In a contact zone of two closely related species, males of *F. hypoleuca* lost their conspicuous, highly contrasting plumage and resembled females. Interestingly females in the contact zone preferred males with a dull plumage over males with a contrasting plumage (the opposite preference as found outside the contact zone). In this case, sexual selection might have reduced conspicuousness.

Sexual selection might be able to accomplish what speciation by reinforcement cannot. Recent work suggests that sexual selection could facilitate sympatric speciation

by means of two runaway processes pulling a population apart into two pre-zygotically isolated populations (Higashi *et al.* 1999). Auklets (Alcidae) are a potential case for speciation by sexual selection (Jones 1999). The mechanism described by Higashi *et al.* (1999) is unlikely applicable to this clade, however, because the elaborate head plumes characteristic for Crested Auklets (*Aethia cristatella*) are also favoured by Least Auklets (*Aethia pusilla*) (Jones, and Hunter 1998).

Sensory exploitation

An alternative, non-adaptive hypothesis for the benefit of conspicuousness is sensory exploitation. According to this theory mating preference need not be adaptive, but instead can arise as a side-effect of sensory or neural architecture that has evolved for different reasons (Ryan 1990; Ryan *et al.* 1990). While often difficult to test experimentally, pre-existing receiver biases can explain the evolution of complex mating rituals that are difficult to explain with any other signalling theory (Ryan 1998).

While the mechanism of handicap selection necessitates the existence of a cost to ensure the reliability, and therefore evolutionary stability, of a signal, the Fisher process and sensory exploitation could involve neutral signals that do not carry an associated cost. However, each process could be driven to the extreme until a physiological limit is reached. Since this physiological limit will vary individually, condition-dependence could be observed nevertheless.

Phenotypic variability

Sexually selected traits are often found and thought to be more variable than purely functional traits (Alatalo *et al.* 1988; Fitzpatrick 1997; Jones *et al.* 2000; Cuervo, and Møller 2001). Extensive polymorphisms and gradual variations are found in many organisms. Such polymorphisms can be based on phenotypic plasticity (Pigliucci 2001) or genetic variation. Mechanisms maintaining genetic variation have been debated since the birth of modern genetics (Dobzhansky 1970). Polymorphisms of plumage pigmentation in birds are rare but widespread amongst different families (Lank 2002; Galeotti *et al.* 2003). Evolutionary mechanisms to produce the plumage variability found within a population include secondary contact resulting in unstable transient polymorphism, ecological fitness cline, heterozygote advantage, negative assortative mating, and negative frequency dependent processes such as selection for individual recognition (Lank 2002).

Selection for individual recognition

In some highly social species, it can be advantageous if individuals recognise each other. Social hierarchies, for example, could be established once and would not have to be contested in costly fights. Selection could lead to the evolution of multiple ornaments which would neither be correlated to each other nor be correlated to individual quality (Dale *et al.* 2001) but simply aid in recognition.

Least Auklet

The auks (Alcidae) are a distinct family of pursuit diving birds with 23 currently recognised extant species (Gaston, and Jones 1998; American Ornithologists' Union 2000; Banks *et al.* 2003). Within the auks, auklets form the tribe Aethiini, a distinct monophyletic group with Fraterculini (puffins) as the most likely sister group (Friesen *et al.* 1996). Like most members of the Charadriiformes, auks are sexually monomorphic to the casual observer. In contrast to many other seabirds, however, auklets are adorned by a variety of sometimes bizarre feather plumes, bill plates and crests.

The Least Auklet (*Aethia pusilla*) is a highly gregarious seabird breeding on remote islands in the Bering Sea and Sea of Okhotsk. Within the Bering Sea it is the most abundant seabird (Stephensen, and Irons 2003). Least Auklets are the smallest members of the alcid family, diurnal and socially monogamous. Amongst alcids, even among seabirds in general, Least Auklets have an unusually variable alternate (breeding) plumage. Variable alternate plumages are also found in *Brachyramphus* murrelets and Parakeet Auklets (*Aethia psittacula*).

Prior work on auklet ornamentation and sexual selection

A considerable number of studies have already been conducted on the evolution of ornaments and sexual selection in auklets. On St. Paul Island, a principal component analysis (PCA)-based index of ornament expression was weakly correlated with a condition index, but only in one out of three years (Jones, and Montgomerie 1992). There was no clear line between assortative mating and disassortative mating in relation to

ornamentation. Disassortative mating was observed with some ornaments and assortative mating with others. Amongst the latter was ventral mottling and size (Jones, and Montgomerie 1991). Ventral mottling was also related to social dominance (Jones 1990) and the frequency of remating, with light birds being more likely to retain their mate in a subsequent year (Jones, and Montgomerie 1991). Model experiments have shown a mating preference for brighter-than-average red bills, larger-than-average auricular plumes (Jones, and Montgomerie 1992) and artificial crests that are present only in related species (Jones, and Hunter 1998). The latter study thereby showed a pre-existing mating preference in Least Auklets for ornaments not present in the species, supporting the sensory exploitation hypothesis.

Their elaborate facial ornaments let Auklets stand out amongst other seabirds. The display of these ornaments is accompanied by highly complex social interactions and vocalisations (Jones 1993a, b). In Crested Auklets, mutual sexual selection has been demonstrated for their crest (Jones, and Hunter 1993). While not yet studied, there is no reason to believe that mutual sexual selection does not occur in the other auklets as well, although not necessarily to the same degree.

Aim and structure of this thesis

The main goal of this thesis is to investigate the evolution of ornaments and plumage variability in Least Auklets. Pursuant to this goal I present five chapters written as individual papers for publication in international journals. Some repetition is inevitable because of this format. First, I examined all seabird species for the evolution

of the pattern of dorsally dark, ventrally light plumage, which, following Cairns (1986), I shall refer to as the "tuxedo pattern". To infer the ancestral state, I mapped the evolution of plumage patterns onto a phylogenetic tree. I then used phylogenetic regression to test three main hypotheses: camouflage through countershading, UV-protection, and social selection.

Before examining ornament expression in Least Auklets, I investigated the species' breeding biology on Buldir Island, to provide necessary background information. I quantified chick growth, fledging age, and breeding success, and tested whether my data fits the predictions of Ydenberg *et al.*'s (1995) model. To put these data into a wider context I compared the Least Auklet's size and fledging age with that of the other auklets and puffins.

A central question in behavioural ecology has been whether ornamentation is related to some form of individual quality. Performance during take-off in escape from a predator has many characteristics that would suggest this measure to be more suitable than popular mass or condition indices. I tested the repeatability of several measures of take-off performance, measured from digital video.

Armed with this new tool I compared the expression of two structural ornaments, bill knob and auricular plume length, and the degree of ventral mottling to take-off acceleration, mass, hematocrit, and leucocrit as measures of individual quality. Linear modelling using AIC as a model selection criterion helped to find a model with a suitable set of covariates amongst year, date, sex, and age.

Finally, I addressed the interaction between Least Auklets and their principal aerial predator, Glaucous-winged Gulls (*Larus glaucescens*). To test whether the auklets' socially dominant white plumage could be a handicap in interactions with the gulls, I presented experimentally manipulated realistic models for gulls to attack, compared plumage and mass between Buldir and an island without gulls, and correlated take-off acceleration with plumage mottling.

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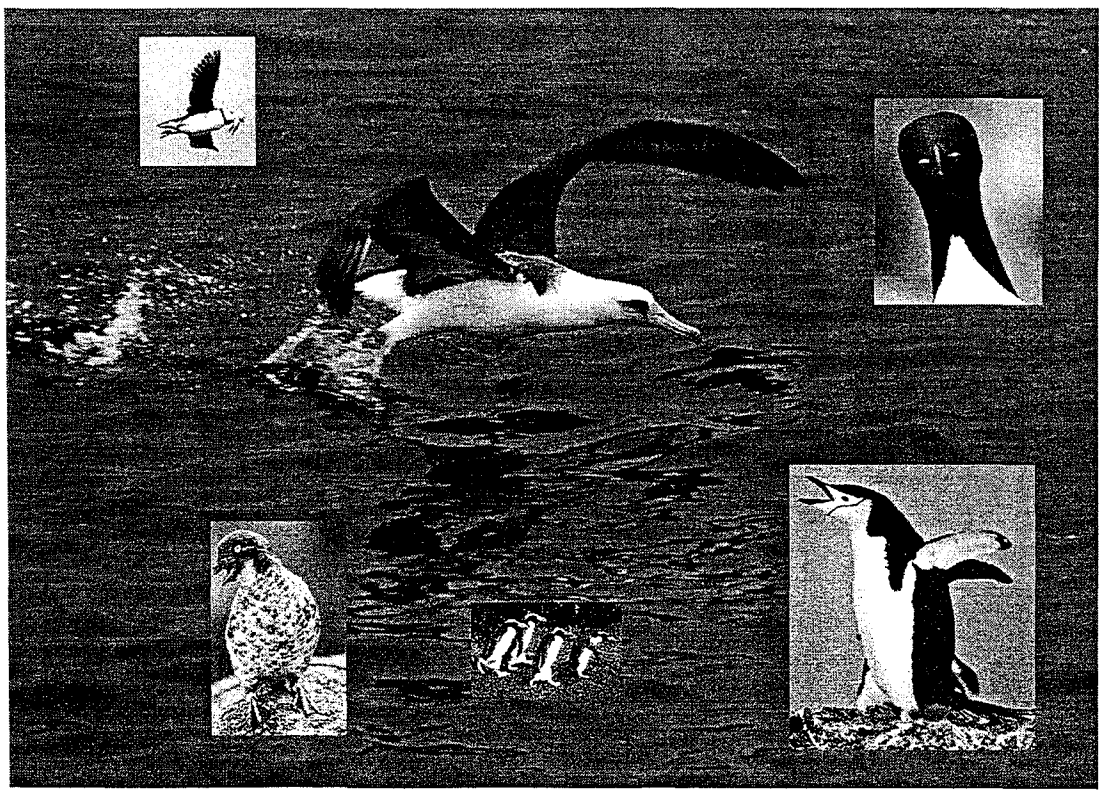
CO-AUTHORSHIP STATEMENT

This thesis is built around five main chapters, each of them written as a paper for publication in an international journal (some of them are already submitted). Three of these papers are co-authored by Ian Jones, one of my supervisors. Ian provided guidance throughout this project, including suggesting I work on plumage variation and conduct a predation experiment with gulls. It was my responsibility, however, to design the details of this experiment. Ian and Ted Miller provided guidance and advice throughout the process of compiling this thesis, including edits, comments and suggestions on the text. All field work, data analysis, and preparation of the manuscripts were my own work, unless acknowledged so in the individual papers.

Chapter 2.

The evolution of seabird plumage patterns – was Darwin right after all?

Martin Renner



Abstract

Marine organisms from plankton to whales, and in particular seabirds, commonly display a black dorsal, white ventral "tuxedo pattern". I test three groups of hypotheses regarding the evolution of this pattern: protection of feathers and skin, camouflage, and social selection. If protection from UV radiation is an issue in the evolution of the tuxedo pattern, we predict a latitudinal gradient in back tone with tropical species having the darkest backs. Countershading in the form of aggressive mimicry predicts differences in plumage pattern between different foraging strategies and prey objects depending on camouflage needs. Protective mimicry predicts differences in plumage pattern with body size. Social selection predicts frequent changes of facial plumage characteristics over evolutionary time. I tested these hypotheses using a classification of plumage tones mapped onto a phylogenetic tree. From this I deduced that most seabird taxa had light-vented and dark backed ancestors. The current pattern of seabird plumages is does not reflect predictions of the camouflage hypothesis. Using phylogenetic regression I found birds at high latitude have slightly but significantly lighter backs than birds at low latitudes ($F = 7.31$, $df = 1, 209$, $P = 0.0074$), supporting the UV or thermal protection hypothesis. There was, however, strong evidence that the evolution of plumage pattern is linked to social selection.

Introduction

A simple but almost universal pattern of dark dorsal and light ventral side seems to prevail amongst pelagic animals (e.g. bioluminescent plankton, Great White Shark (*Carcharodon carcharias*), Manta Ray (*Manta birostris*), Blue-fin Tuna (*Thunnus thynnus*), crocodiles (Crocodilia), loons (Gaviidae), penguins (Sphenisciformes), murres (*Uria* spp.), and whales such as Humpback Whale (*Megaptera novaeangliae*), and Orca (*Orcinus orca*). I will follow Cairns (1986) and call this pattern the "tuxedo pattern". Textbook knowledge (Nelson 1980 pp. 57-59) has it that this pattern is an adaptation to camouflage its bearer both from above, when viewed against the dark ocean, and from below, when viewed against the bright water surface or against the sky (Cairns 1986). Thayer (1896; 1909a; 1909b) explained the function of this pattern as "countershading". Lighter tones in the shade and darker tones in direct light are supposed to offset each other, creating a uniform impression when viewed from the side and, against the background a camouflaged effect. "Countershading" or self-shadow concealment (Kiltie 1988; Edmunds, and Dewhirst 1994) is frequently used to explain the tuxedo pattern. It is important to differentiate between the pattern (tuxedo) and the function (countershading). The term "tuxedo pattern" seems to be particularly appropriate for high-contrast transitions from the light ventral to the dark dorsal side, as found in many marine organisms. For the countershading effect to work, the full tuxedo pattern is needed. A light ventral side and a dark dorsal side each by themselves can still provide camouflage from below, and from above, respectively.

Darwin (1871, p. 494) as struck by how many aquatic bird acquired a white plumage, compared to terrestrial birds, which he viewed as a conspicuous trait. He argued that all perfectly white, intensely black, or pied plumages, as found in gulls, gannets, tropicbirds, or herons, evolved through sexual selection. In his view these plumages are conspicuous and could help conspecifics find each other at sea, e.g. to share a food resource.

Besides selection for colour pattern as a social signal or camouflage, two further major groups of hypotheses have been proposed to explain the evolution of animal colouration: selection for the physiological benefits of pigments, and selection for colour patterns to enhance the animal's own vision (Burtt 1981). The latter appears unlikely here, but dark back could have evolved for physiological reasons such as thermoregulation (Hamilton, and Heppner 1967; Heppner 1970; Walsberg *et al.* 1978), UV protection (Burtt 1979), protection from abrasion (Barrowclough, and Sibley 1980), or to enhance plumage drying rate (Burtt 1981). The ventral side might simply remain white because it does not require any protective pigments, allowing the bird to save the physiological cost of synthesizing additional pigments.

The story of the countershading hypothesis as an adaptive explanation for the tuxedo pattern is so compelling, however, that (as pointed out by Kiltie (1988)) even Gould (1985), one of the foremost critics of adaptive story-telling (Gould, and Lewontin 1979), falls into the adaptationist's trap. Even though the countershading hypothesis has now been around for about a century, there have been only a few experimental tests. De Ruiter inverted caterpillars (several species, including *Smerinthus ocellata*, *Laothoe*

populi, Mimas tiliae) so their light side would face upwards and found that they were more susceptible to predation by Eurasian Jays (*Garrulus glandarius*) than caterpillars in the normal position (de Ruiter 1956). Similarly, birds depredated countershaded caterpillars significantly less often than inverted or plain green caterpillars (Edmunds, and Dewhirst 1994).

More recent experiments found that "artificially countershaded prey" had an advantage over reverse-countershaded (all-light and all-dark individuals) with some avian predators but not with others (Speed *et al.* 2004). Three-spine Sticklebacks (*Gasterosteus aculeatus*) showed both stronger and earlier responses to black than to white model gulls flown overhead (Phillips 1962). In a similar experiment with painted Black-headed Gulls (*Larus ridibundus*) naturally-white birds had higher success rates catching fish than black painted birds (Götmark 1987). Yet, a recent review found little evidence for the mechanism of countershading other than in a few marine organisms with extreme camouflage (Ruxton *et al.* 2004).

All these studies address the problem only on a single species and provide evidence for current utility. Although the tuxedo pattern seems to be ubiquitous at first, there are also numerous exceptions, e.g. Tufted Puffins (*Fratercula cirrhata*), and Sperm Whales (*Physeter catodon*) are ventrally and dorsally all dark, Common White-Terns (*Gygis alba*), and Snow Petrels (*Pagodroma nivea*) are entirely white. If a white underside functions to camouflage its bearer, it seems odd that many rodents have white ventral sides while their predators would view them almost exclusively from above. Even flatfish display the same pattern (while their "upper" side is really lateral) despite their

benthic lifestyle. Above mentioned exceptions raise doubt whether the tuxedo pattern really evolved for camouflage, as supported by Gould, or whether camouflage is just a by-product and white is just the default tone of seabirds' feathers that have no need for deposited pigments. While there are several good hypotheses to explain light ventral sides, the numerous dark-bellied seabirds appear paradoxical.

In this paper I will investigate the evolution of the tuxedo pattern in seabirds. There is no monophyletic group of seabirds. There are, however, several avian lineages, which adopted a specialised aquatic, largely marine, lifestyle. These groups, to which I will refer as "seabirds", include the Procellariiformes, Sphenisciformes, Gaviidae, the former "Pelecaniformes" (gannets and boobies, cormorants, anhingas, pelicans, frigatebirds, and tropicbirds), and within the Charadriiformes the phalaropes (Scolopacidae), and all the Stercoraridae, Laridae, Sternidae, Rynchopidae, and Alcidae. Sea ducks were not included here because they differ substantially from the classical seabirds (e.g. they are sexually dimorphic) and because limited phylogenetic information is available. I will survey the range of seabird plumages to see how widespread the tuxedo pattern is.

Interspecific comparisons require a correction for phylogeny since shared ancestry leads to a lack of independence between species. The comparative method (Clutton-Brock, and Harvey 1984; Felsenstein 1985; Harvey, and Pagel 1991; Harvey, and Purvis 1991) solves this problem by contrasting a taxon with its respective sister taxon rather than with all taxa simultaneously. I will map the evolution of plumage traits on the seabird phylogeny to infer the plesiomorphic plumage of different seabird clades and employ the comparative method to test the following hypotheses for the evolution of

seabird plumage: 1. White undersides function as aggressive camouflage, making it either easier to capture fish, or as defensive camouflage concealing a swimming or diving bird from aquatic or aerial predators (camouflage hypothesis). 2. Dark pigments protect the bird from UV radiation, mechanical abrasion, or extreme temperatures (protection hypothesis), 3. Seabird plumage pattern evolved to facilitate social interactions (social hypothesis).

Predictions

Although fish are larger and thereby more profitable prey items than plankton, they also have better vision and have more potential for escape. Piscivorous seabirds can therefore be expected to require more camouflage than planktivores. I might also find differences in plumage between plunge divers, surface feeders, and pursuit divers due to their different strategies used to capture prey. Defensive camouflage should be more important to small, vulnerable species than to larger species with fewer predators.

Dark pigments provide protection against harmful UV radiation and make feathers more resistant against abrasion. Annual UV doses are several times higher in the tropics than in temperate or polar regions (Sabziparvar *et al.* 1999). It follows from the UV-protection hypothesis that dark backs will be more common in low-latitude species than in high-latitude species if UV protection is important for determining the shade of seabird plumage. Dark plumages also absorb more radiation than white plumages (Hamilton, and Heppner 1967; Lustick 1969). However, because radiation penetrates a light plumage deeper than a dark plumage, cooling through convection affects dark plumages much more than light plumages with the result that, especially in windy conditions, a light

plumage may be warmer than a dark one (Walsberg *et al.* 1978). If plumage patterns are driven by thermoregulation needs I would expect a cline from dark plumages in the tropics to light plumages in polar regions, similar to the UV protection hypothesis. In contrast to the UV protection hypothesis we might expect the whole body to be affected, because the back-scattered radiation is biased towards longer wavelengths and UV radiation might therefore be less of a problem. .

Finally, the rapid drying hypothesis (Burtt 1981) predicts that birds in colder climates are darker because they will have a greater need to dry quickly.

Assuming that most social interactions occur during the breeding season, we can predict that characters important for social interactions are expressed more strongly in alternate (adult breeding) plumages than in basic (winter) or juvenal plumages. Reversing this logic we might expect that characters, which are most prominent in alternate plumages, would be involved in social interactions. Furthermore, these characters would be most likely located around the face and on the bird's ventral side rather than on the dorsal side because birds tend to face each other in social interactions. With few exceptions (e.g. Millar *et al.* 1994) seabirds are monogamous and rates of mate retention are known only for a few species. These variables are therefore unsuitable to test whether social selection affects plumage patterns. There is evidence, however, that characters used in social interactions undergo rapid divergent evolution between closely related taxa (Pomiankowski, and Iwasa 1998), while purely functional traites are more likely to be conserved. I therefore predict finding an increased number of evolutionary changes in characters shaped by social selection.

Methods

Phylogenetic data were collected from the literature (see Appendix) to piece together a phylogenetic tree of all major seabird taxa (n = 269). I visually scored plumages on a scale from 1 (all white) to 5 (all black) by examining published photos and paintings from field guides and handbooks (Harrison 1985, 1987; del Hoyo *et al.* 1992, 1996; Enticott, and Tipling 1997). The other possible scores were 2 (mostly white), 3 (medium-grey) and 4 (mostly dark). For mottled and partial coverages, a proportion of area covered by black feathers was estimated by eye and translated into a grey value (1 to 5). I estimated a separate score for the belly, the throat, and the back (including folded wings).

I gathered information on size (mass, length, wingspan), distribution, diet, and breeding biology from the literature (del Hoyo *et al.* 1992, 1996). Where only ranges were given I used the mean of the extremes. Mass and length were combined to "size" by extracting the first major axis from a principal component analysis. Distribution was scored separately for breeding and non-breeding seasons on a scale of 1 to 5 for tropical, subtropical, temperate, subpolar, and polar. For analysis I used the mean of the two ranks. I coded diet data into three classes: plankton, squid, and fish. I used diet both as a present-absent variable for piscivores and as a ranked variable assuming that fish have the greatest escape potential, followed by squid, followed by plankton. Mean ranks were used for species with a diverse diet. Foraging methods were categorized as either plunge diving, surface feeding, or pursuit diving. Unless specifically stated I used belly or back of definitive basic plumage as the dependent variable. I used MacClade (version 3.05,

Maddison, and Maddison 1992) to map the evolution of plumages onto the phylogeny and CAIC (version 2.6.8b) (version 2.6.8b, Purvis, and Rambaut 1995) for analysis of phylogenetic contrasts. Branch lengths were assumed to be equal.

Results

White is by far the most common belly and throat shade for seabirds in any plumage (Figure 2.1). Black is the most common shade for the back, although intermediate shades are common too. Mapping the three plumage characters onto the phylogeny indicates that a light belly is the plesiomorphic state for most major seabird taxa (Figure 2.2). Notable exceptions are Frigatebirds (ambiguous), Terns (ambiguous), and the "core Pelecaniformes" (cormorants, darter, and boobies – ambiguous, Figure 2.2). There were 61 independent unambiguous events when bellies (definitive basic plumage) changed in shade, only four of which involved a switch back from dark to lighter shades (Figure 2.3). Ancestral states for the back were inferred to be shades between medium grey and black.

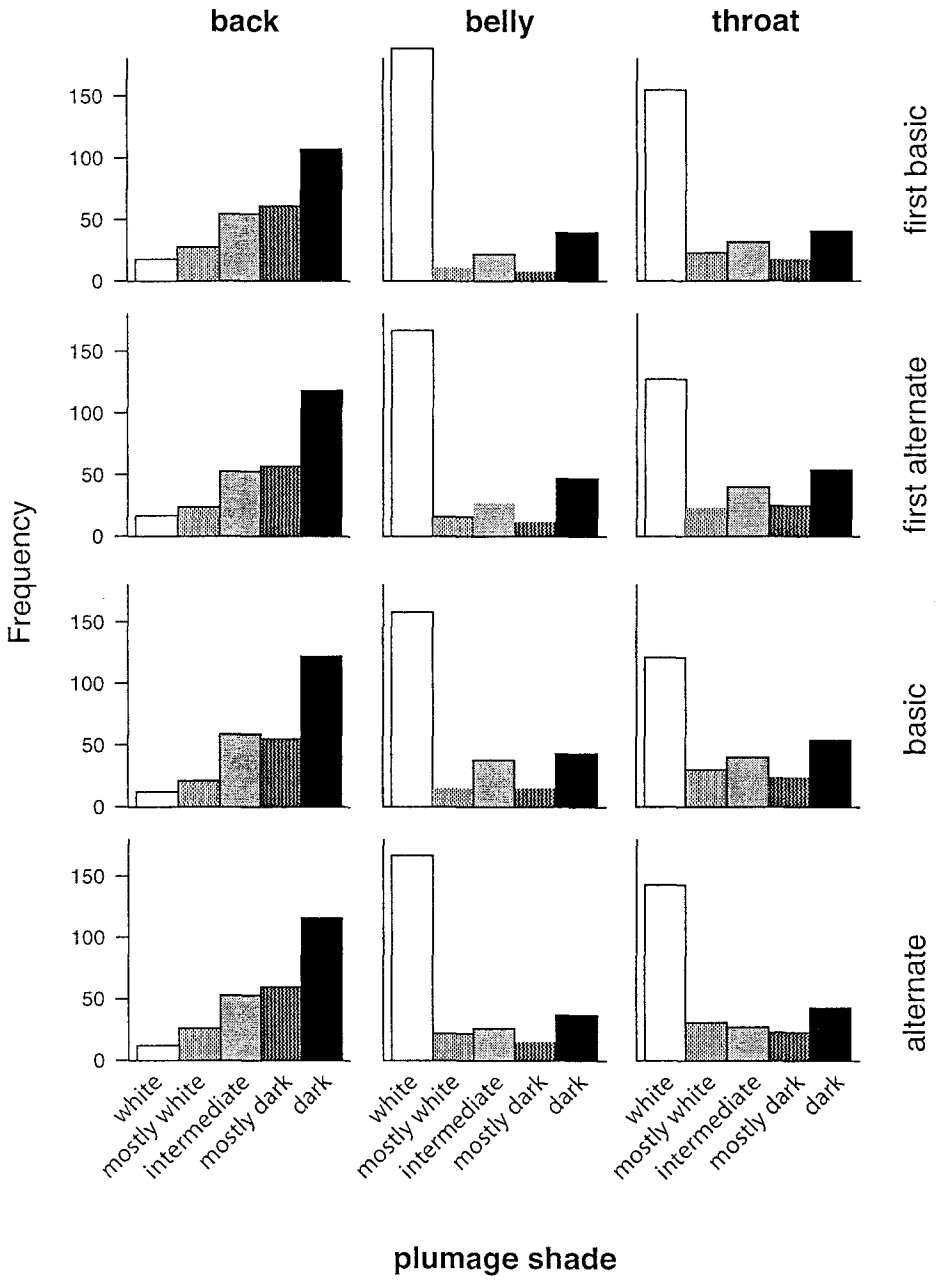


Figure 2.1 Survey of seabird (269 species) plumage shades (from white to dark) on back, belly, and throat for first-year birds and adults in basic and alternate plumage. Despite some exceptions, most seabird species have the tuxedo pattern of white bellies and dark backs (not taking phylogeny into account).

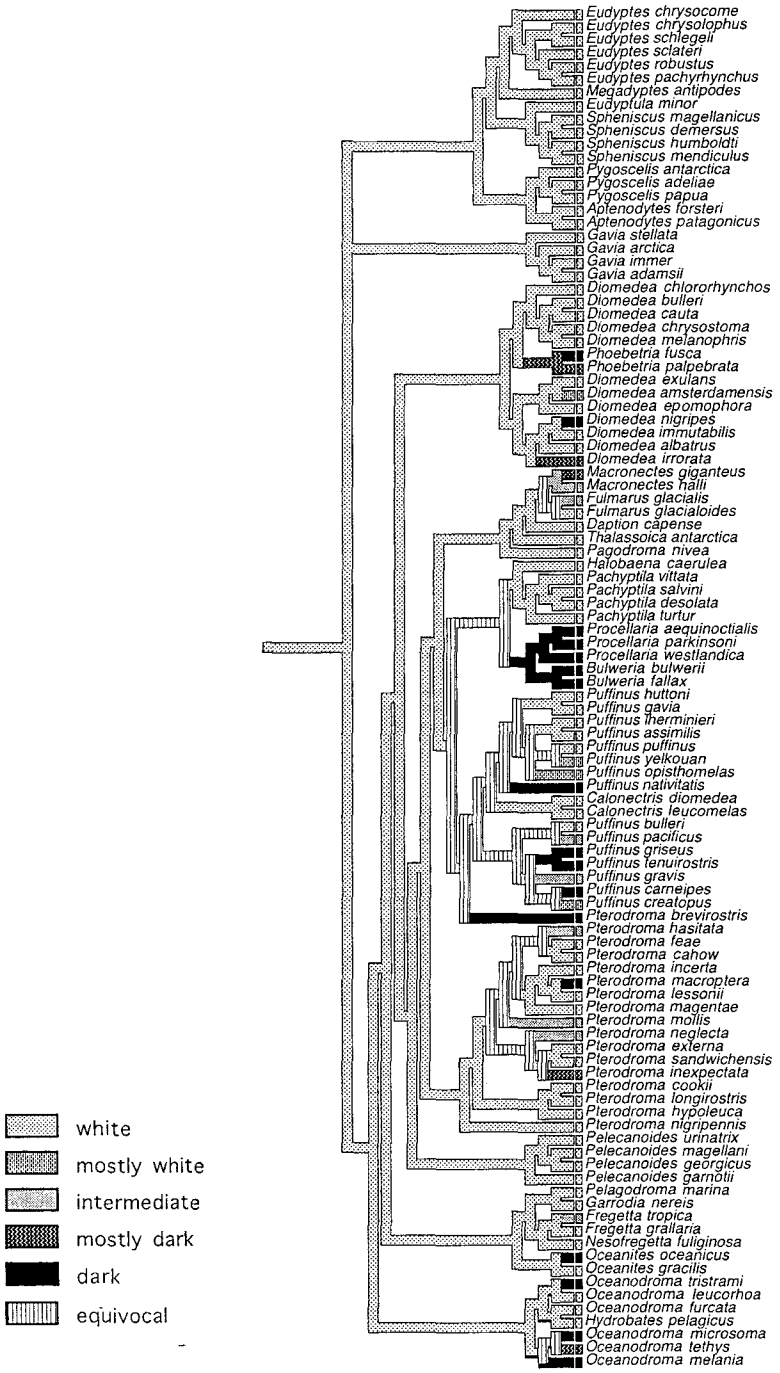
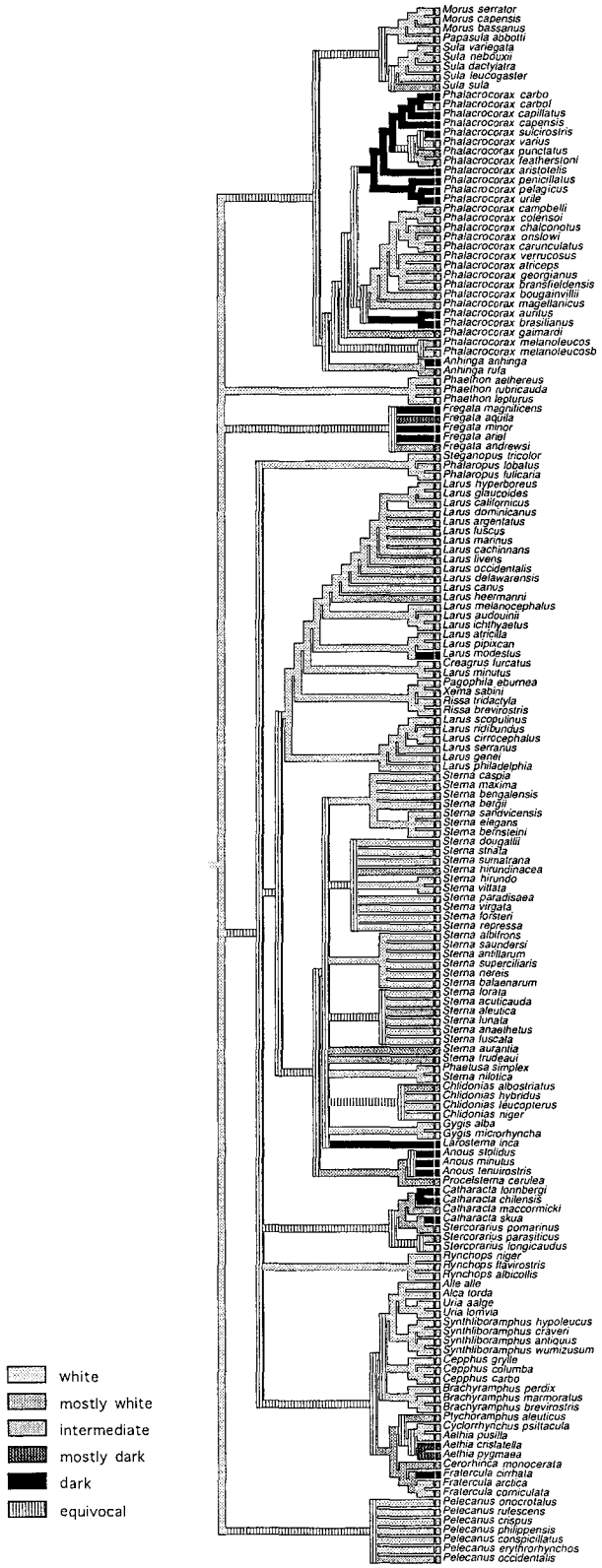


Figure 2.2 Shade of belly of definitive basic (adult non-breeding) plumage mapped onto composite phylogeny. Procellariiformes, Gaviiformes and Sphenisciformes were placed as a sister group to a polytomy of the remaining seabird taxa.

Figure 2.2 continued



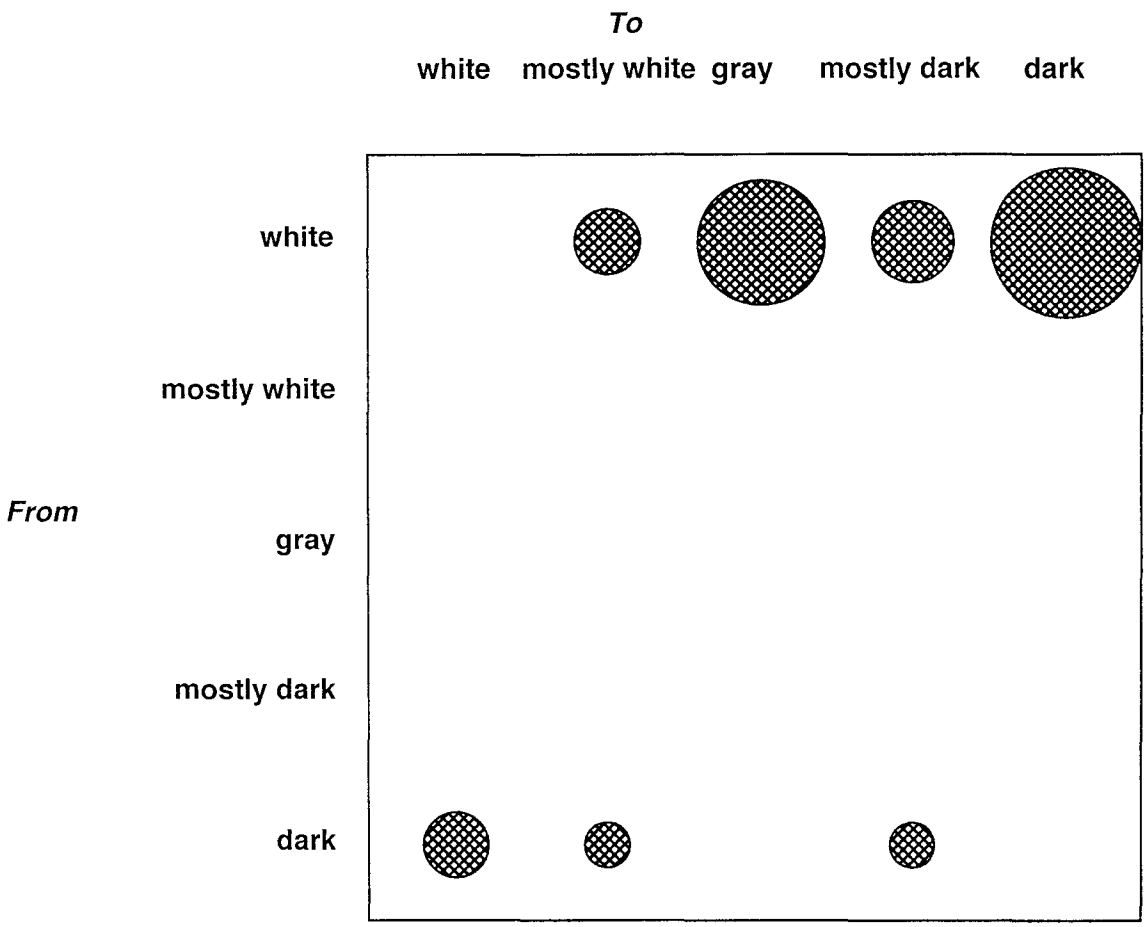


Figure 2.3 Frequency of unambiguous changes between states of definitive basic belly plumage of 269 seabird species (total = 61 changes, area of circle is proportional to number of changes).

Camouflage hypothesis

Contrary to the prediction of the camouflage hypothesis there was no correlation of diet and the shade of belly plumage (aggressive camouflage), either when treating diet as a ranked variable (fish, squid, plankton) or when looking at fish compared to non-fish

eaters ($F = 0.31$, $df = 1, 76$, $P = 0.58$, and $F = 0.16$, $df = 1, 30$, $P = 0.69$, respectively). Body size was also not correlated with ventral plumage shade either ($F = 0.25$, $df = 1, 170$, $P = 0.62$). I expect plunge divers to profit more from camouflage than pursuit divers because the former ambush their prey whereas the latter is more likely to out-swim their prey. Instead I found that plunge divers tend to be ventrally darker than non-plunge, pursuit divers ($F = 3.95$, $df = 1, 16$, $P = 0.067$, $r^2 = 0.22$). All three tests therefore fail to support the camouflage hypothesis.

Protection hypotheses

As predicted by the UV-protection, seabirds have significantly darker backs in low than in high latitudes (Figure 2.4, $F = 7.31$, $df = 1, 209$, $P = 0.0074$). The r^2 was only 3%. Although there are all-white species in both polar regions, they do not seem to drive the regression as outliers (Figure 2.4). Assuming that light birds have a thermal advantage over dark birds in cold climates and visa versa, this result also supports the thermoregulation hypothesis. The rapid drying hypothesis predicts an inverse relationship from the one found here and not supported.

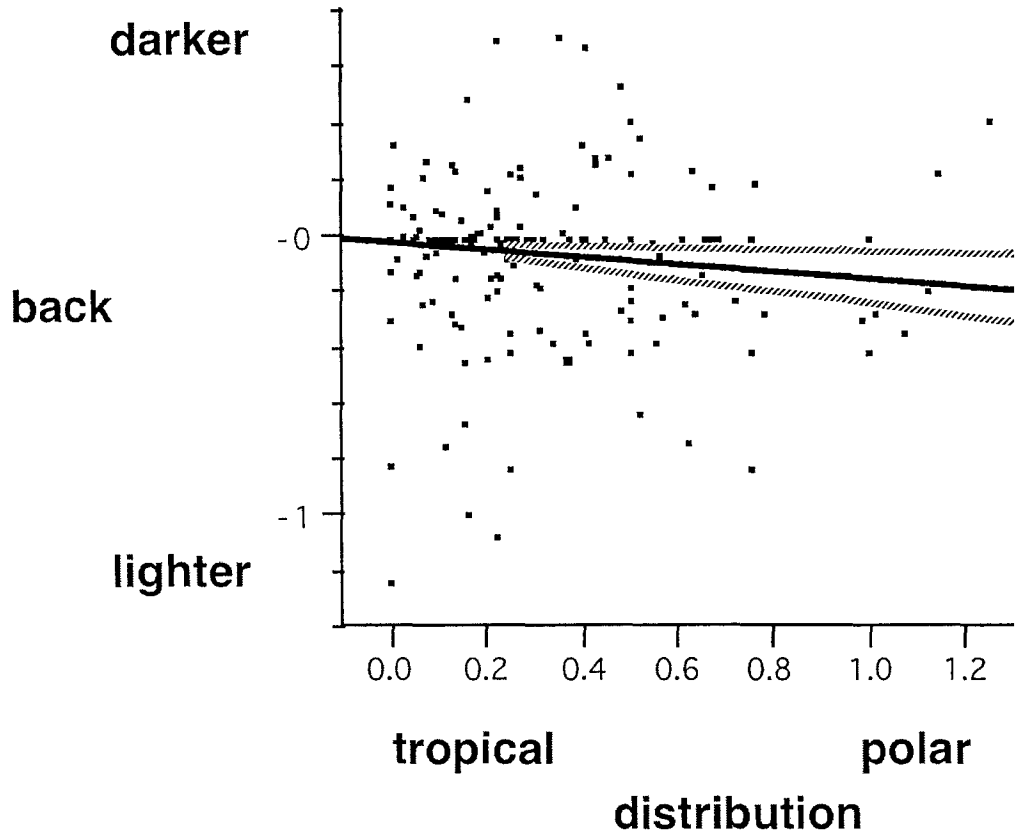


Figure 2.4 Plumage shade in relation to distribution. Back plumage lightens with increased latitude ($F = 7.31$, $df = 1, 209$, $P = 0.0074$, $r^2 = 0.03$) supporting the UV-protection hypothesis.

Social hypothesis

Evolutionary changes were most numerous for throat and belly plumage, which are typically visible to conspecifics when interacting socially, and less for back plumage, which tends to be less visible during social displays. Even greater was the number of evolutionary changes in the neck/face area, the arguably most important area for social

signals in optically orientated organisms. Changes in definitive alternate, or "breeding" plumage were more common than in basic, or "winter", plumage, and more common in first alternate than in juvenal or first basic plumage (Figure 2.5). Most seabird species gather in, sometimes large, colonies to breed. During the non-breeding season, many species still forage in flocks, but disperse much wider than during the breeding season when competition for breeding space can be intense. Juvenile seabirds typically disperse far over the ocean, sometimes for years and probably experience less social interactions than any other age class. In all comparisons, the plumage, which is most likely to be used in social displays, experienced most evolutionary changes, as predicted by the social hypothesis.

Discussion

Using a comparative analysis of the world's seabirds, I tested three evolutionary hypotheses of the seabird "tuxedo" plumage pattern. I found that most seabird taxa probably had light-bellied and dark to mid-tone-backed ancestors - shades that remain by far the most common amongst extant seabird species. Because seabirds represent no single monophyletic group, but rather a collection of taxa adapted to a marine life, many non-seabird taxa have been left out, especially in the higher nodes of the phylogeny. These taxa could influence the reconstruction of ancestral states. There are also uncertainties about the topology of the reconstructed phylogeny, in particular towards the base. These uncertainties are reflected in several polytomies. I expect this analysis to be

robust even towards an incorrect topology at higher taxonomic levels since many character states cannot be unambiguously inferred.

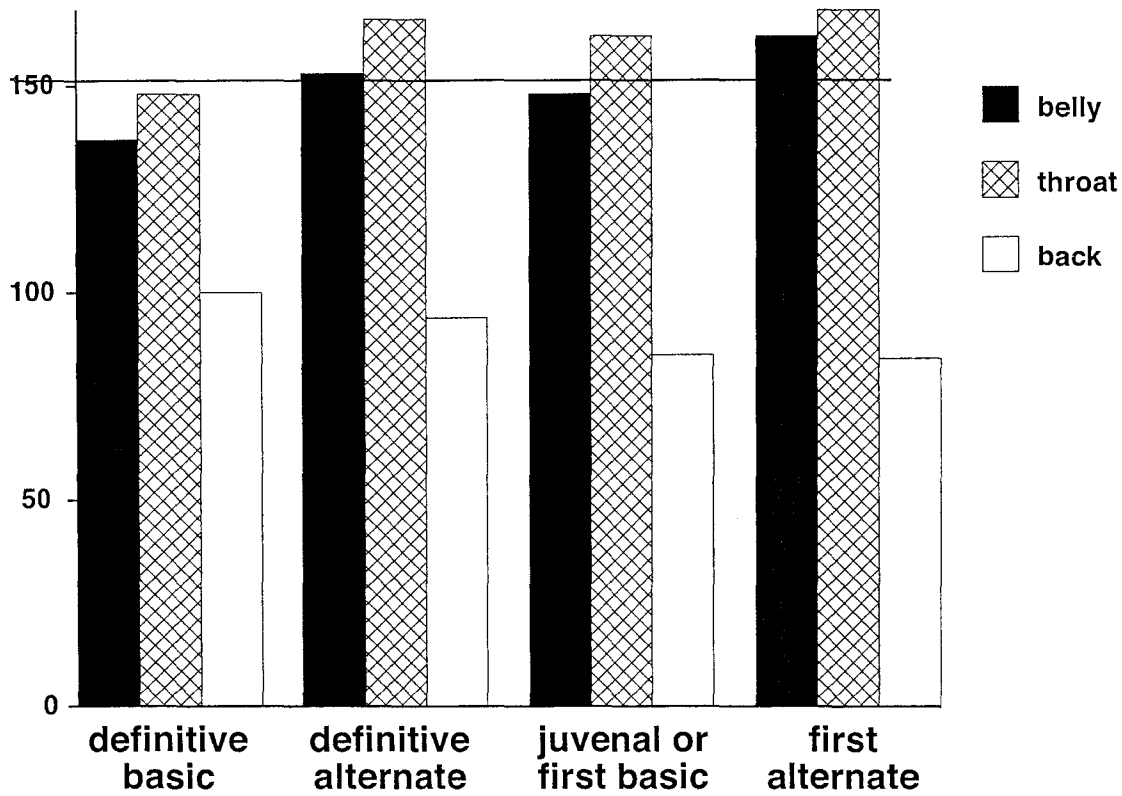


Figure 2.5 Numbers of evolutionary changes at belly, back, and throat in definitive basic, definitive alternate, juvenal or first basic, and first alternate plumages.

There are many pre-conceived notions on what constitutes a conspicuous and a cryptic plumage at sea. In laboratory experiments dorsally white gulls are more successful capturing fish than experimentally blackened birds (Craik 1944; Phillips 1962; Mock 1980; Götmark 1987). The same plumage can be perceived as conspicuous above water (Darwin 1871), although this again might depend on cloud coverage and position of

the sun, which can affect the lighting situation dramatically in a marine environment (Simmons 1972).

Two authors have attempted to test the aggressive camouflage hypothesis of seabird plumage experimentally (Phillips 1962; Götmark 1987). Both concluded that a white ventral side increases the chances of successful capture of fish by comparing natural white birds to black painted birds or models. Besides the general shortcomings of demonstrating current utility as an explanation for ultimate causes, a bird painted artificially black does not seem be a suitable control. To demonstrate that seabirds evolved white bodies for aggressive camouflage it would have been more appropriate to show that white is actually the optimal plumage and not, for example, a shade of grey or even blue. Both studies were conducted under laboratory settings with calm water surfaces. Natural, more disturbed water surfaces will make it more difficult for fish to notice any object above the water surface (Phillips 1962), reducing the beneficial effect of white belly coloration.

I did not find support for either aggressive or defensive camouflage as a driving force behind seabird plumage patterns. By default a keratinous feather is white unless a pigment is synthesised and deposited in it (Tickell 2003). With no counter-acting selection pressures, a white integument develops as the physiologically cheapest option as demonstrated by many cave-dwelling organisms. More promising might be an approach to identify factors associated with dark ventral sides in seabirds. Given white as the default, a claim, that seabirds evolved white bellies as camouflage, should produce some positive evidence explaining some of the variability in seabird plumages. I did not find

such evidence and am not aware of other studies providing such evidence. By contrast, plunge divers tended to be ventrally darker rather than lighter than non-plunge divers, the opposite as expected from the camouflage hypothesis. With white as the cheapest physiological option being the simplest explanation, the camouflage hypothesis does not pass Ockham's razor test, even though it makes for a good story.

I did find a latitudinal trend though with high latitude birds tending to have lighter backs, as would be expected under the UV-protection hypothesis or the thermoregulation hypothesis. A much more detailed study taking local weather pattern and specific distribution data into account, might be able to distinguish between these two, non-exclusive, hypothesis. Such a study might also be able to address the significance of melanin to protect seabird feathers from abrasion.

Sexual selection has been well received as the driving force behind the evolution of an astounding diversity of external appearances with no apparent ecological benefit. I regard the finding that frontal parts of the breeding plumage experienced most evolutionary changes as evidence for social selection, without trying to explain individual cases. Darwin (1871) speculated that a conspicuous plumage could draw attention to conspecifics. His own objection is that this altruistic cause could not have produced a conspicuous plumage through gradual natural selection because it would put the first finder, who has to share its food source, at a disadvantage. This objection might not be valid, however, because at least some birds might be more successful capturing fish when in groups than when alone (Götmark *et al.* 1986).

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Appendix

Taxonomic treatments

In this analysis, I consider as seabirds the loons, penguins, tube-noses, "Pelecaniformes" (excluding shoebill), phalaropes, skuas, gulls, skimmers, terns, and auks. If a detailed phylogenetic hypothesis was available, I excluded those species which were missing in this phylogeny unless they were known sister taxa (as treated in Sibley, and Monroe 1990), leaving me with 269 species.

The phylogenetic relationships between orders of birds are still largely unresolved or at least disputed, despite prolonged efforts by both molecular and morphological

systematicists. None of the available large-scale studies (Sibley *et al.* 1988; Sibley, and Ahlquist 1990; Cooper, and Penny 1997) considered all the orders used in the present study, leaving many of the high order nodes unresolved. The much debated "Pelecaniformes" are treated here, contra to Cracraft (1985), as a polyphyletic group following Hedges and Sibley (1994), Siegel-Causey (1997) and Cooper and Penny (1997).

I treat loons, tube-noses, and penguins as one clade with a basal polytomy (based on Cracraft 1982; Sibley 1990; Paterson *et al.* 1995; Cooper, and Penny 1997). Detailed systematic studies, often based on molecular data are available for penguins (O'Hara 1989; Grant *et al.* 1994; Paterson *et al.* 1995; Edge 1996; Davis, and Renner 2003), tube-noses (Nunn, and Stanley 1998), gannets and boobies (Friesen, and Anderson 1997), cormorants and darters (Kennedy *et al.* 2000), skuas (Cohen *et al.* 1997), gulls (Crochet *et al.* 2000), and auks (Friesen *et al.* 1996). Arrangements within the terns are poorly resolved. I follow Hoffman (1985) in his arrangements of the genera within the terns.

Chapter 3.

Breeding biology of the Least Auklet (*Aethia pusilla*) at Buldir Island, Alaska

MARTIN RENNER AND IAN L. JONES

Abstract

To investigate the consequences to breeding biology of the evolution of small body size, we quantified breeding parameters of Least Auklets (*Aethia pusilla*), the smallest extant pursuit-diving seabird. Field work was conducted at Buldir Island, western Aleutian Islands, Alaska in 2000, 2001, and 2002. We used the apparent estimator for hatching success and Kaplan-Meier survival analysis to estimate fledging success. Measures of chick growth were fitted to Richards curves. Mean productivity was 0.51 (95 % CI: 0.45 - 0.57). Chicks were exposed to the greatest mortality risk during the first seven days after hatching. We found significant inter-annual variation for several morphometric growth parameters, but not for any of the mass growth parameters. Slightly more than half of chicks showed a decline in body mass prior to fledging, averaging 11 % loss of their peak mass. Three out of Ydenberg et al.'s (1995) four predictions were supported: in accordance with the model we found significant negative relationships of hatch date with fledging age and fledging mass, and a positive relationship between fledging mass and maximal mass growth rate. However, we did not find a significant relationship of growth rate with fledging age. Wing length, rather than mass, appears to be a more likely trigger of fledging in Least Auklet. We suggest that the evolution of small size in this species was accompanied by unusually rapid and advanced nestling development and a variety of related behavioural and physiological traits.

Introduction

The Least Auklet (*Aethia pusilla*) is the smallest species in the family Alcidae, the smallest of all pursuit-diving birds and one of the smallest of all seabirds. Amongst pursuit-diving birds, Least Auklets (ca. 80 g) are over 25 % smaller in mass than the next smallest pursuit-diving species, Whiskered Auklet (*Aethia pygmaea*; 108 g) and the South Georgia Diving Petrel (*Pelecanoides georgicus*; 93 g (Prince, and Jones 1992)), and two and a half orders of magnitude smaller than the largest (Emperor Penguin *Aptenodytes forsteri*; 25-40 kg). Storm-petrels are lighter than Least Auklets, but no other seabird has a smaller wing-span (del Hoyo *et al.* 1992; 1996). Their extreme size must place the species in a special situation near the limit of what is physiologically and ecologically possible, making its biology especially important to investigate. While a large body of work exists documenting selective forces towards the evolution of large size (e.g. Davis, and Speirs 1990; Burger 1991), surprisingly little is known about mechanisms that lead to the evolution of small size (Blanckenhorn 2000).

The Least Auklet is largely endemic to the Sea of Okhotsk and the Bering Sea (Jones 1993) and it is by far the most abundant of all seabirds in the Bering Sea (Stephensen, and Irons 2003). Least Auklets feed on zooplankton (especially Calanoid copepods), breed in dense colonies, lay a single egg in rock crevices and provision their chick until it is nearly adult size (Roby, and Brink 1986; Jones 1993).

While some aspects of this species' biology are well studied, (e.g. foraging habitat - Springer, and Roseneau 1985; diet - Hunt, and Harrison 1990; copulation behaviour -

Hunter, and Jones 1999; survival rates - Jones *et al.* 2002), relatively little is known about its breeding biology, with only three one- to two-year studies published (Sealy 1981; Roby, and Brink 1986; Piatt *et al.* 1990). Sealy (1981) concentrated on the morphology of breeding crevices and provided information on fledging mass from St. Lawrence Island in the northern Bering Sea. Piatt *et al.* (1990) presented data on breeding success, mortality causes and chick growth from the same site. Roby and Brink's (1986) study provided information on egg composition, hatching success and chronology, chick growth, and feeding rates from St. George Island, Pribilof Islands, central Bering Sea, over two years in the early 1980s. In contrast to the St. Lawrence and Pribilof Islands, which harbour native populations of Arctic fox (*Alopex lagopus*), most of the Aleutian islands were devoid of mammalian predators before introductions were made by humans. The native avifauna of Buldir Island was fortunate, compared to that of many other Aleutian Islands, because fur-farmers never established foxes there. On islands where foxes and auklets overlap, predation of adult auklets is ubiquitous. Prior to the present study therefore, little information was available on factors affecting breeding success, chick growth, and the timing of chick mortality, especially from a site free of terrestrial predators.

Buldir Island is located in the western Aleutian Islands and separated by > 100 km wide passes from the nearest islands to the west and east. The sea is ice-free year round and snow cover has usually receded well above the Main Talus colony site by the time auklets arrive in the spring. Many auklet nests can be found within comparatively easy reach of the talus surface, making this a particularly suitable to study breeding biology.

On Buldir, roughly 100,000 Least Auklets breed on the Main Talus colony, together with ca. 300,000 Crested Auklets (estimated in mid-1970s, Byrd *et al.* 1983), smaller numbers of Parakeet Auklets (*Aethia psittacula*), and large numbers of Horned Puffins (*Fratercula corniculata*), Whiskered Auklets, and storm-petrels (Byrd, and Day 1986; Stephensen, and Irons 2003).

Detailed, quantitative accounts on the breeding biology of the other *Aethia* auklets have already been published from Buldir (Hipfner, and Byrd 1993; Fraser *et al.* 1999; Hunter *et al.* 2002). So far, the only information published on the breeding biology of Least Auklets from the Aleutians concerns phenology and the structure of the breeding crevices (Knudtson, and Byrd 1982). Quantitative data on chick rearing are missing, however. Since 1988, the Alaska Maritime National Wildlife Refuge has monitored auklet productivity on Buldir on an annual basis (Dragoo *et al.* 2003). We studied the breeding biology of Least Auklets on Buldir Island during the summers of 2000, 2001, and 2002. Our objectives were to quantify breeding phenology, breeding success, timing of chick mortality, chick growth, and length of the brooding period to evaluate the fit to Ydenberg et al.'s (1995) model of fledging mass variation and to evaluate the selective forces responsible for the characteristics of Least Auklet's breeding biology relative to other auklets (Auks, tribe *Aethiini*). The main predictions from Ydenberg et al.'s (1995) model are that faster-growing nestlings fledge younger and heavier than slower growing chicks, and later-hatched chicks fledge younger and lighter (Ydenberg 1989; Ydenberg *et al.* 1995).

Study Area and Methods

Field methods

Fieldwork was conducted from late May to early August in the years 2000, 2001, and 2002 at the Main Talus auklet colony on Buldir Island (52°21'N 175°56'E), western Aleutians Islands, Alaska. The island is home to the largest and most diverse assemblages of seabirds in the Aleutians, possibly in the whole Northern Hemisphere (Byrd, and Day 1986). Main Talus consists of a mostly barren, north-facing boulder slide with an average slope of 45°. Apart from Main Talus, auklets also breed on the south side of the island, on a small section of coastal cliff on the south side, and on two offshore rocks at the west end of the island.

Each year we searched for active auklet breeding crevices throughout the season using small flashlights from 1400 hours to no later than 2100 hours (HAST - about 2.5 hours before local solar time), when there was no auklet surface activity. Crevice entrances were marked with a unique code painted on surrounding rocks. To avoid reduced breeding success due to human disturbance (Piatt *et al.* 1990), we took care to move about the talus quietly, avoided shining flashlights straight at adult birds, and visited the area near crevices only when necessary. In contrast to other studies (Roby, and Brink 1986; Piatt *et al.* 1990), we also avoided moving any rocks near a crevice and refrained from excavating crevices. In Crested Auklets, following this protocol did not measurably reduce breeding success at Buldir (Fraser *et al.* 1999). During May and early June we checked crevices every three to six days; once adults were observed carrying

food in their gular pouches we checked crevices every three days. We avoided touching adults to detect hatching but rather looked for egg shells, listened for chicks' begging calls, and looked for the change in the adults' posture that occurs between incubation and chick-brooding. Often, chicks were observed directly. Because our protocol was aimed at minimizing disturbance, an exact hatching date could not be determined in every case.

We caught the brooding adult within the first or second day after hatching using a wire crook, banded, measured, and blood sampled it. The bird was then carefully returned it to its chick. The following day, we caught the second adult. If an adult was missed this way, we returned at night (2300 to 0400 HAST) to capture the missing partner in the pair. Chicks found dead in the crevice were examined for wounds, subcutaneous fat, and wetness of the down.

Statistical methods

Since most crevices were found after laying we had no way of ageing eggs before they hatched without unduly disturbing the parents. Apparent hatching success is a biased estimate leading to an overestimation, unless all crevices are found before nest failure occurs. We compared apparent hatching success with estimates derived using the Mayfield (1961; 1975) method, which makes the extra assumption of a constant failure rate during incubation. We assumed a crevice was used if we observed an adult incubating an egg or if an adult was present on at least two consecutive visits. To evaluate standard error and confidence intervals, we used the bootstrap with 10,000 replicates. For the purpose of applying the Mayfield method we assumed an incubation period of 30 days (Sealy 1984; Piatt *et al.* 1990).

Many crevices were difficult to inspect and often an egg could not be seen. We estimated a hatch date only for those crevices for which we actually saw the egg and then the chick within six days. Hatching and failure/fledging dates were assumed to be the midpoint between visits, using half days if the visit interval was an uneven number of days. The estimated hatching/failure date could therefore be up to three days off the true date.

Chick survival was analysed using survival analysis (Kaplan, and Meier 1958; Allison 1995; Renner, and Davis 2001). This was similar to the Mayfield method, with the main difference that not a constant but an age dependent daily survival rate was estimated. We thereby avoided the assumption of constant survival rate made by the Mayfield method. If a dead chick's body was found, it was carefully examined for signs of trauma, reserves of subcutaneous fat, and condition of its down plumage. Subcutaneous haemorrhaging, bite-marks, or external bleeding indicated a violent death, possibly by other auklet species. If a chick disappeared after having lost most of its down and developed almost fully grown primaries, we assumed that it had fledged. In some cases it was not possible to catch and measure the chick on every visit. If a chick was older than the mean fledging age when it disappeared, or if the last wing measurement was within 80 % of the mean adult wing length, we assumed it had fledged.

We assumed chicks to have died if they disappeared when younger than the lowest fledging age observed (22.5 days). Chicks that disappeared at an age between lowest and mean (29 days) observed fledging age were assumed to have the same chance of survival as chicks of the same age that remained under observation. We treated chicks that had

not fledged by the time we left the island in the same way. Censoring means that a chick was only used in the calculation up to a certain date and then disappeared or died of unrelated causes. Its future, unknown or hypothetical, fate was assumed to be equal to the average risk experienced by the remaining population under study. Fledging success was then calculated from the cumulative survival probabilities over age from hatching to the mean fledging age. To identify phases when chicks were most vulnerable to various risks, we plotted hazard functions smoothed with a kernel smoother with a bandwidth determined by MSE minimization (Muller, and Wang 1994; Wang 1998). Bandwidth was optimized for all causes combined and then applied to each risk factor to be estimated separately. To include chicks with unknown hatch date (defined as above), we used growth curves, in particular wing, to narrow down a hatching date. While some chicks remained at the spot in the crevice where they hatched until they fledged, others moved around underneath the rocks and often evaded capture. In those cases, chicks were not encountered during every crevice check. Chicks that were missed once, then reappeared, and then disappeared for good were censored as well.

We multiplied our estimates of hatching success and fledging success to yield an estimate of productivity (chicks fledged per egg laid). Standard error and confidence intervals were calculated using the bootstrap on the product of hatching and fledging success.

Chicks were measured when their accompanying adults were caught during the brooding phase. They were measured again after they were no longer brooded during the day and every three days thereafter. Chicks were either caught by hand or extracted using

a wire crook. Chicks, particularly older ones, commonly tried to escape capture by retreating deeper into the talus. In these cases, fewer measurements were available than for other chicks. We omitted chicks from the sample if less than four measurements were available if the last measurement was at an age less than 16 days. Chicks that failed to fledge were also excluded. The following measurements were taken: body mass to the nearest 1 g using a Pesola spring scale, head and bill length, tarsus length (parallel method) using dial callipers to the nearest 0.1 mm, and wing length (including feathers) using a zero-stop ruler to the nearest mm. All measurements were taken by MR.

We analysed chick growth by fitting non-linear growth functions to individual chicks. To find the best fitting model, we fitted Richards curves (Richards 1959) to the combined data of all chicks. Richards curves have the form

$$L(t) = L_{\infty}(1 + e^{-k(t-t_0)}r)^{\frac{1}{r}}$$

with $L(t)$ being the growth variable at time t

L_{∞} the asymptotic value of the growth variable

t_0 the inflection point of the curve

and k relative growth rate at the inflection point.

Richards curves are a family of functions. By changing the shape parameter r, the commonly used von Bertalanffy $L(t) = L_{\infty}(1 - e^{-k(t-t_0)})$ (r = -1/3), Gompertz $L(t) = L_{\infty}e^{-Ce^{-k(t-t_0)}}$ ($r = 0$), and logistic $L(t) = \frac{L_{\infty}}{1 + e^{-k(t-t_0)}}$ ($r = 1$) growth curves can be expressed as a Richards curve (Figure 3.1). The flexibility of Richards curves offered both advantages and disadvantages. A close fit could be achieved that also incorporated

the shape of the curve, and shapes not covered by Gompertz, von Bertalanffy, or logistic curves. However, the added shape parameter m is difficult to fit, since it is closely correlated with the relative growth rate k, especially when only a limited number of observations are available (Zach 1987). To compromise between limiting the number of parameters to fit and fitting the appropriately shaped curve, we fitted Richards curves to the combined data of all surviving chicks of known age. Individual data points are not independent when a curve is fitted to the combined data of all chicks. This means that the error on the fit was underestimated, but the fit was not biased. We then applied the value of r found in the global fit as a fixed parameter to fits of individual birds. Because growth data of mass, in contrast to all morphometrics considered, showed a marked increase in variation with age, we log-transformed mass and fitted to a log-transformed model.

Since we kept r constant for each individual fit, we were left with the parameters L_∞,, k, and t_0 to fit. Of these, only t_0 has an immediately obvious biological interpretation (inflection point of the curve, which is the age of maximal growth rate). From the remaining parameters L_∞,and k we derived two measures that are biologically more meaningful: m^* is the maximal growth rate (occurring at the inflection point) and is given by $m^* = L_\infty k(1+r)^{-1-\frac{1}{r}}$ (equations modified from Jorgensen 1981), and fledging size taken from the predicted size at the day of fledging. In case of $t_0 < 0$ days, we used the expected growth rate at hatching $m(t=0) = \frac{\partial L}{\partial t} = L_\infty e^{-k(t-t_0)} k(1+e^{-k(t-t_0)}r)^{-1-\frac{1}{r}}$.

While not as extreme as in some Procellariiformes with extended nesting periods (Warham 1990, 1996), Least Auklet chicks can undergo a slight decline in body mass prior to fledging (Sealy 1981; but also see Roby, and Brink 1986). Huin and Prince (2000) present an approach to fit a model to this type of curve. However, due to the added flexibility, even more parameters are necessary than for the Richards curve. Instead we truncated mass data of each individual to include one datapoint after peak mass was reached. To investigate the extent of pre-fledging mass loss, we quantified how many days passed from the day with highest mass until fledging and what percentage of the maximum mass was lost at the last time the chick was measured before fledging.

To visualise the relationships between the growth parameters of different measurements we used a hierarchical cluster analysis based on Spearman rank correlations (Sarle 1990; Harrell 2004). We used a generalized linear (ANCOVA) model to test the predictions from Ydenberg *et al.*'s model. As a covariate we added the year as a factor. We first tested for a significant interaction term and removed this term from the final model if it was not significant. All statistical calculations were coded in R (R Development Core Team 2004) with the packages "boot" (Davison, and Hinkley 1997), "Hmisc" (Harrell 2004), and "MASS" (Venables, and Ripley 2002). Means are reported ± standard error of the mean unless stated otherwise.

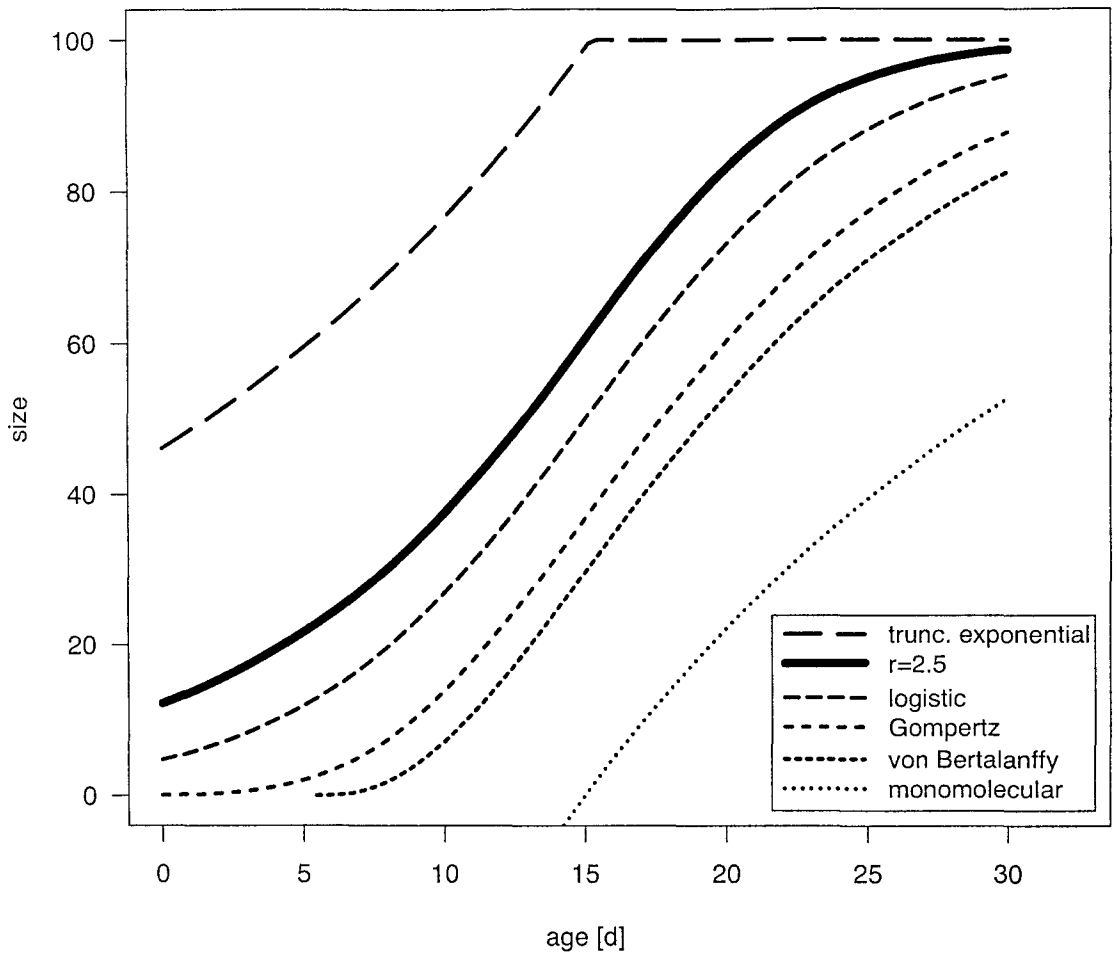

Figure 3.1 Comparison of Richards curves with different shape parameters *r*: truncated exponential growth ($r \to \infty$), best fit for Least Auklet mass ($r = 2.5$), logistic ($r = 1$), Gompertz ($r = 0$), von Bertalanffy ($r = -1/3$) and monomolecular growth ($r = -1$). All curves are scaled to have the same maximum growth rate at the same age (15 days), and the same asymptote (100).

Results

Phenology

The shape of the distribution of hatching dates closely resembled a normal distribution in 2000 but was bimodal in 2001 and 2002, when a small number of chicks hatched during a small second peak in July (Figure 3.2). There were no significant differences in mean hatching date between years though (ANOVA, df = 2, 90, F = 0.78, P = 0.462). Observed hatching dates ranged from 18 June to 14 July (mean = 26 June ± 0.54 days, n = 93). In both 2001 and 2002 one and three eggs, respectively, hatched almost a month after the first eggs recorded to hatch (Figure 3.2).

Hatching success

Different methods of calculating hatching success each showed their inherent biases but did not differ greatly, with estimates for all years combined ranging from 0.805 to 0.852 (Table 3.1). To check the assumption of constant survival rate made by the Mayfield method, we plotted a hazard function of egg-survival. As a laying date we used 27 May, i.e. 30 days prior to the mean hatching date. While this will be inaccurate for some eggs, based on the distribution of hatching dates (Figure 3.2), we expect most egg ages to be within 5 days of the assumed age. The hazard function of egg-survival (Figure 3.3) is flat at close to zero for most of the incubation period, but shows a steep rise beginning about 30 days after mean lay date (i.e. breeding attempts tended to fail late in incubation), conflicting with the main assumption of the Mayfield method, which was conceived to handle a constant risk of predation.

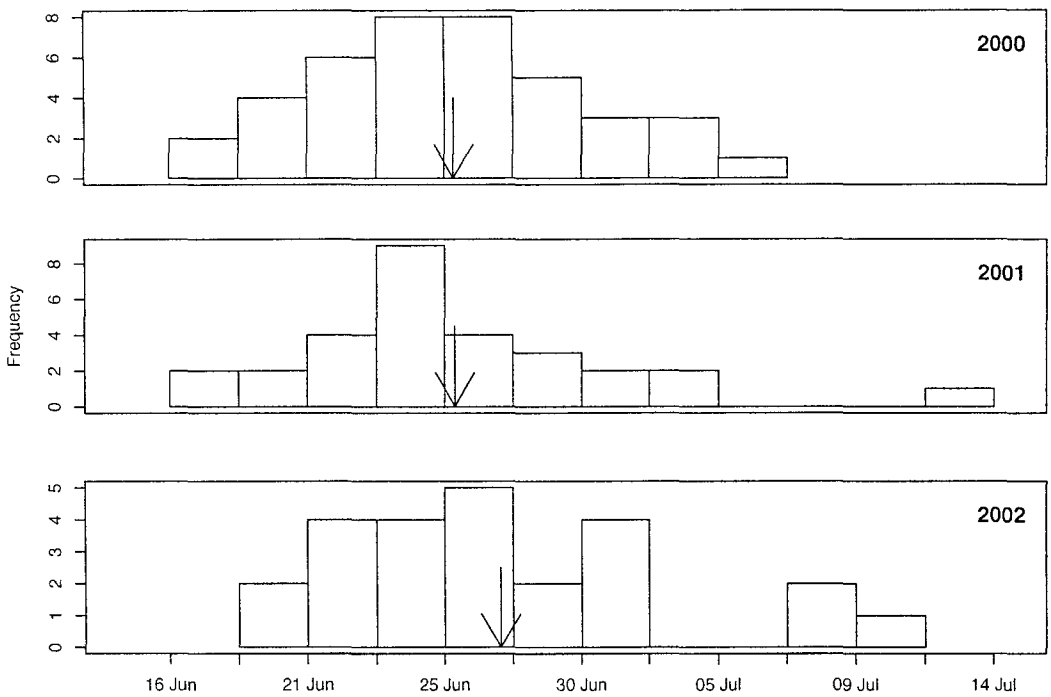

Figure 3.2 Hatching dates of Least Auklets (*Aethia pusilla*) in during the years 2000 (N = 40), 2001 (N = 29) and 2002 (N = 24) on Buldir Island, Alaska. Arrows indicate the mean hatch date for each year.

Table 3.1 Estimates of hatching success of Least Auklets on Buldir Island (2000-2002 combined). Apparent hatching success does not correct for nests that failed before they could be discovered. The threshold method disregards nests that were discovered after 15 June. The Mayfield method assumes a constant daily nest failure rate and a 30 day incubation period to calculate hatching success. Estimates of hatching success differ by up to 4.7 % depending on calculation method.

method	mean	se	95 % CI	
apparent	0.843	0.0227	0.800	0.890
threshold	0.852	0.0317	0.793	0.918
Mayfield	0.805	0.0254	0.756	0.855

Length of brooding phase

For a few days after hatching, at least one adult was continuously present brooding the chick. This brooding stage ranged from less than a day to 12 days, with an average of 4.69 ± 0.33 days (n = 60). Once a chick was left by itself for the day, it would sometimes be brooded for one further day but after that, none were guarded by an adult during the day. At night, however, one adult, sometimes two, were often present with the chick long after the day-brooding phase. The latest recorded age at which a chick was brooded at night was 23 days.

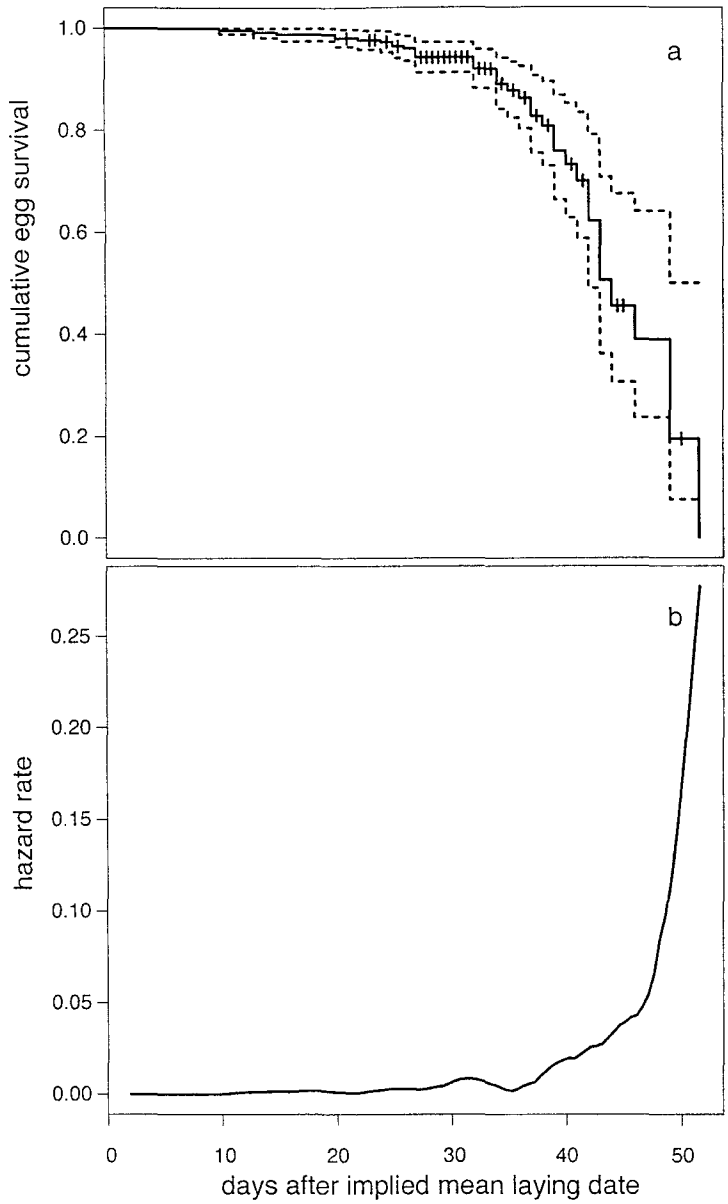

Figure 3.3 a) Cumulative survival (± 95 % confidence interval) of Least Auklet eggs. By 52 days after mean laying date, all eggs that did not hatch yet, were abandoned or had disappeared. b) The corresponding hazard function, smoothed using a constant-bandwidth kernel smoother. In violation of the main assumption of the Mayfield method, the rate of breeding failure was not constant but remained low until after the expected hatching time and rose sharply thereafter.

Chick survival

Age of fledging ranged from 22.5 to 36.5 days after hatching (mean 29.09 ± 0.56, n = 39, CV = 12 %). Fledging success (as determined by the predicted survival probability at the mean fledging age 29 days) was 0.586 ± 0.053 (95 % CI from 9,999 bootstrap replicates: 0.491 - 0.700) (Figure 3.4). No confirmed mortality events were recorded after the age of 23.5 days. Mortality risk was greatest during the first seven days, during which disappearances, exposure to rain, injuries, and unknown causes played a significant role (Figure 3.5). Starvation was recorded in only three instances when the chick was close to the age of fledging (Table 3.2, Figure 3.5). In most cases, the cause of death could not be determined, however, because the chick either disappeared or because there were no obvious indications of what caused the chick to die.

Productivity

Based on the above estimates for hatching success and fledging success, we estimated productivity at 0.5127 ± 0.0304 (95 % CI from 9,999 bootstrap iterations: 0.45 - 0.57) fledged chicks per laid egg using apparent hatching success and 0.494 ± 0.035 (95 % CI: 0.39 - 0.53) fledged chicks per laid egg using the Mayfield method.

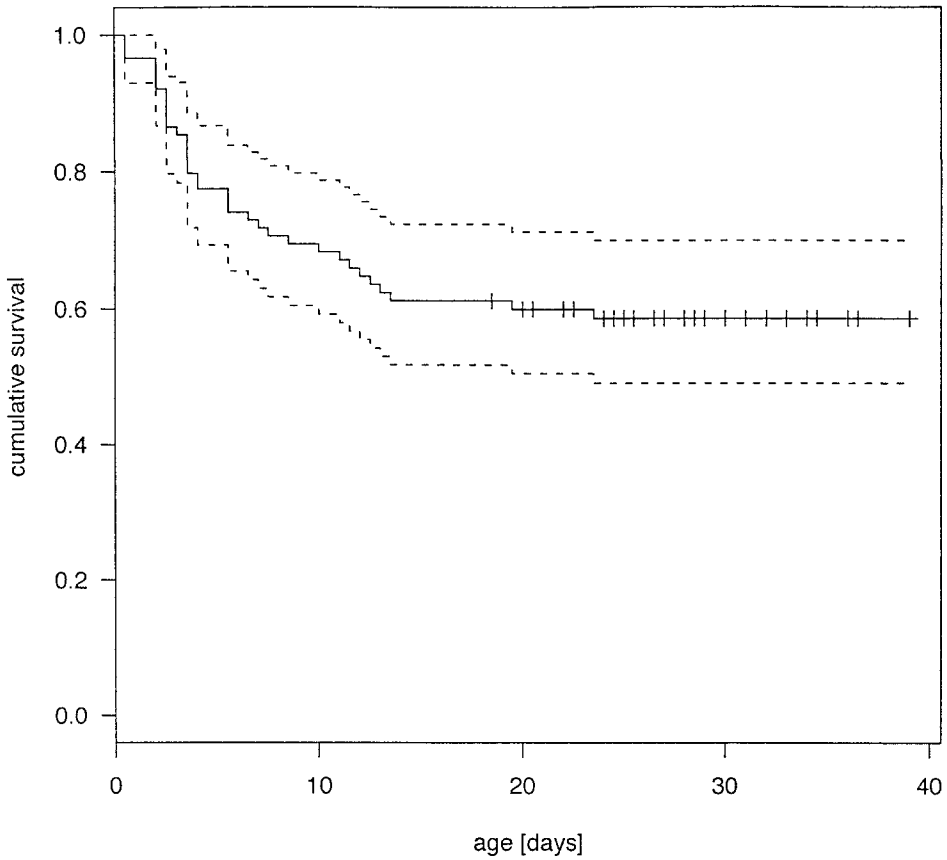

Figure 3.4 Cumulative survival curve (± 95 % confidence interval) of Least Auklet nestlings from hatching to fledging.

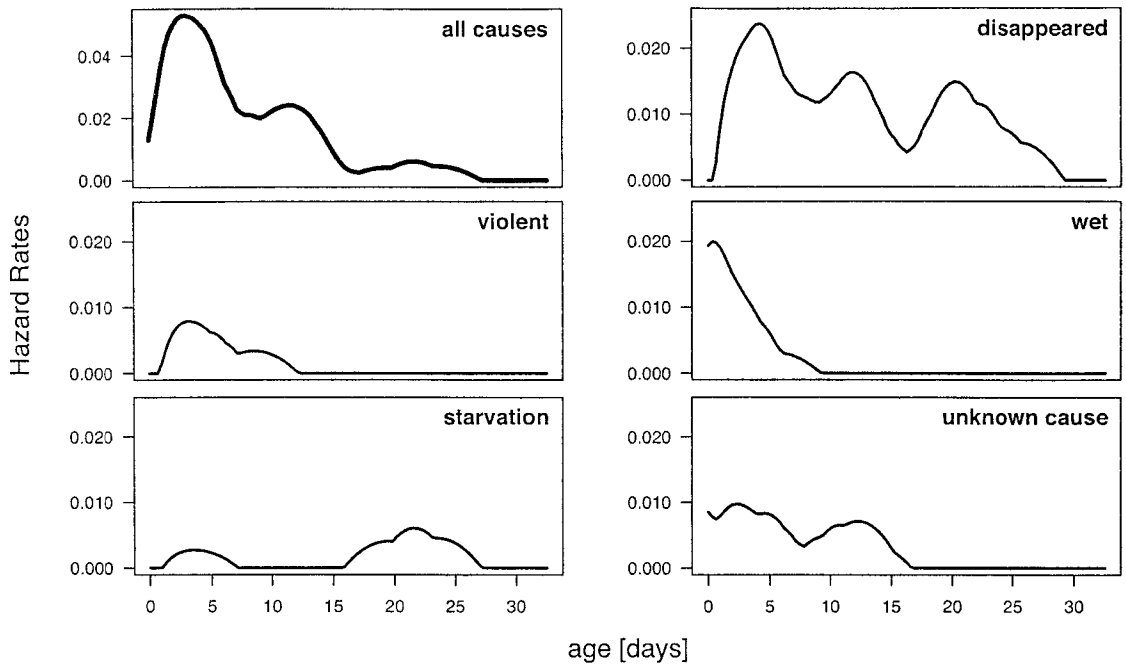

Figure 3.5 Hazard rates of competing risks to Least Auklets chicks. Noisy hazard rates were smoothed with a global kernel smoother .

Table 3.2 Estimated survival rates of Least Auklet chicks from hatching to fledging age (29 days post-hatch) partitioned into recognized mortality causes. Presented are survival estimates and the number of observed mortality events (n).

	survival	se	95 % CI		n
all causes	0.586	0.0531	0.491	0.700	36
disappeared	0.786	0.0480	0.697	0.886	16
violent	0.946	0.0266	0.895	0.999	4
wet	0.929	0.0280	0.876	0.986	6
starvation	0.946	0.0312	0.886	1.000	3
unknown	0.901	0.0360	0.833	0.975	7

Chick growth

Body mass and wing length, showed sigmoidal growth curves (Figure 3.6). The best fitting Richards curve for mass had a shape parameter *r* of 2.49, similar to wing length (Table 3.3). A Richards curve with an *r* between 2 and 3 shows a slower increase in growth rate and reaches peak growth rate later, closer to the asymptote than an equivalent logistic (or Gompertz) curve (Figure 3.1). Head+bill and tarsus lengths fitted a Richards curve well but displayed only the late stage of the curve, with the estimated inflection point prior to hatching (Figure 3.6, Table 3.3). The best fitting Richards curve for head+bill and tarsus lengths resembled a logistic and Gompertz curve, respectively. Head+bill length and especially tarsus lengths reached close to adult size soon after hatching. Mass and measurements of nesting adults are summarised in Table 3.4 for comparison.

During the nestling period, Least Auklet chicks' skeletal measures increased by less than 50 %, but mass increased to over five times the hatching mass (f:h, Table 3.3). As indicated by the CV, fledgling size was most variable for mass, but maximal growth rate and timing of growth varied most for tarsus and head+bill measurements. Among all growth parameters, age at maximal growth of mass and wing were most closely correlated (Figure 3.7). Fledging mass and fledging head+bill size were also closely correlated. Maximum tarsal growth rate was closest correlated with the age of maximum growth of tarsus. All these relationships were positive.

Mass recession was observed in 51.5 % of all chicks before fledging (Figure 3.8). Mass declined for up to 9 days. Of those chicks that did show a pre-fledging decline in mass, the mean number of days of decline was 5.28 ± 0.33 days (n = 50). These chicks lost on average 10.97 % ± 1.03 % (n = 50) of their peak mass before fledging (Figure 3.9).

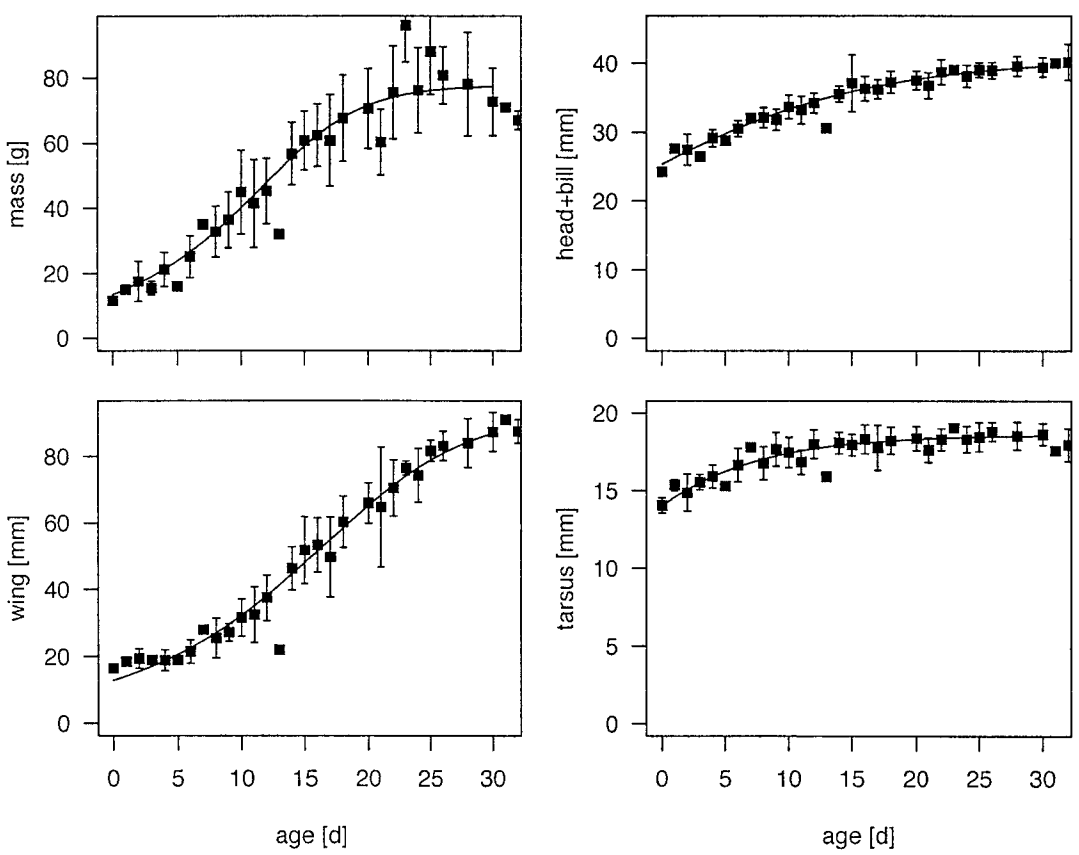

Figure 3.6 Richards curves fitted to measurements of Least Auklet (*Aethia pusilla*) chick growth. Shown are one-day averages ± SD of 98 fledged chicks combined. We have only one chick at age 13 days, which makes this data point look like an outlier.

Table 3.3 Least Auklet chick growth parameters from Buldir Island. Parameters are derived from Richards curves fitted by non-linear least squares regression. The shape parameter *r* was fitted to data for all chicks combined and then held fixed at the tabulated value for individual fits. All measurements are in g or mm, rates are in g/day or mm/day. f:h is the ratio of hatching size to fledging size (means at age 0-3 and 27-30, respectively). %ad expresses the fledging size as a proportion of the mean of the respective measurement taken on breeding adults. A negative age of maximum growth means that the extrapolated inflection point of the underlying Richards curve lies before the hatching date. For these chicks, the hatch date was used to estimate maximal growth rate, rather than the age at the inflection point.

	all chicks combined					individual fits											
						fledgling size					maximal growth rate				age of maximal growth			
	r	a	k	t	f:h	mean	SE	% ad	CV	n	mean	SE	CV	n	mean	SE	CV	n
mass	2.49	77.7	0.29	11.8	5.40	81.3	1.63	98 %	19.2%	91	4.78	0.12	24%	91	12.2	0.31	24 %	92
head+bill	1.1	40.7	0.10	-4.7	1.49	39.3	0.16	92 %	3.9%	91	4.37	0.27	58%	91	-2.5	0.446	-170 %	91
wing	1.99	93.1	0.19	16.6	4.66	86.4	0.79	86 %	8.7%	91	3.73	0.05	13%	91	16.55	0.32	19 %	91
tarsus	-0.16	18.6	0.15	-8.9	1.28	18.7	0.10	100%	4.3%	60	2.86	0.34	91%	60	-7.77	1.357	-135 %	60

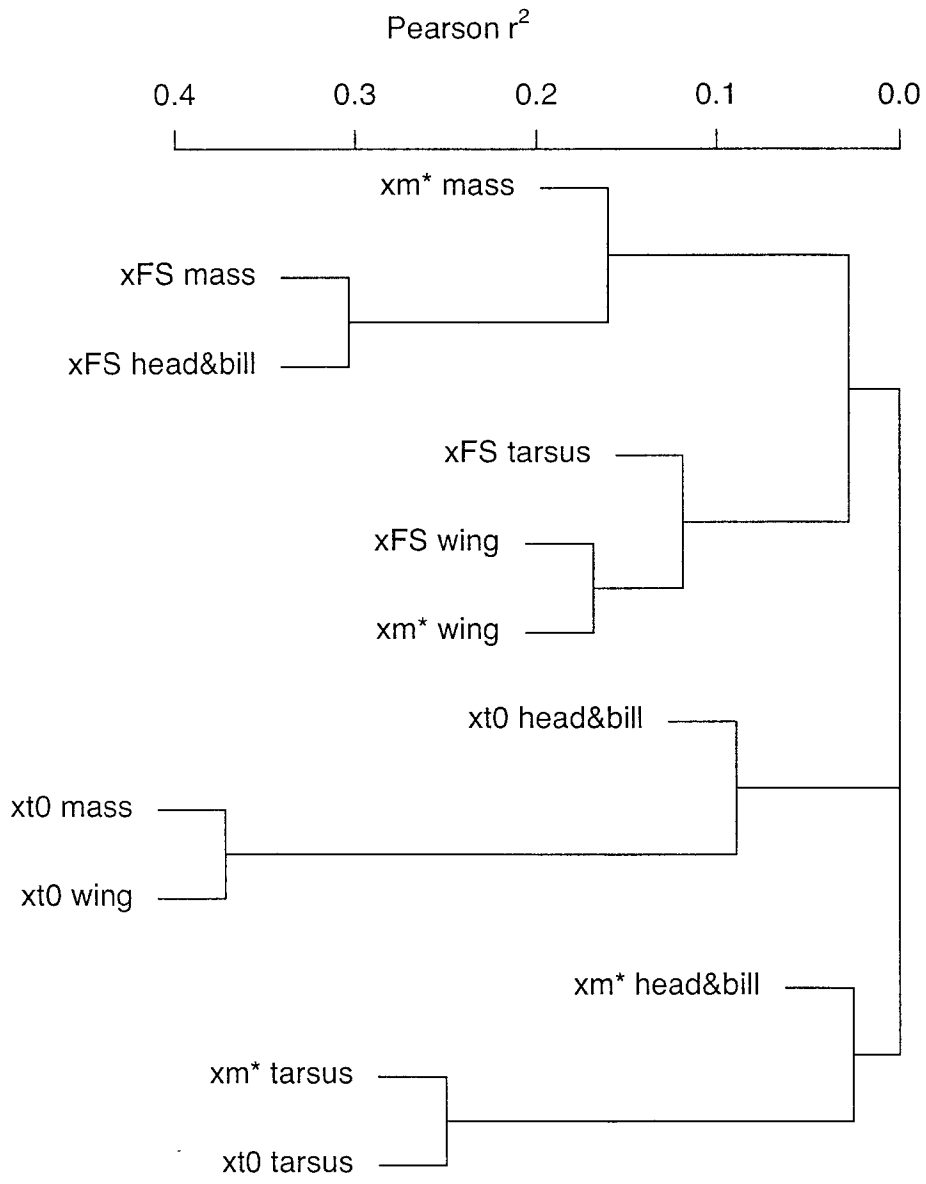

Figure 3.7 Cluster analysis of Spearman correlations between Least Auklet (*Aethia pusilla*) chick growth parameters (FS: fledging size, m*: maximal growth rate, t_0: age of maximum growth). All parameters of mass growth are closely related to the respective parameter of wing growth.

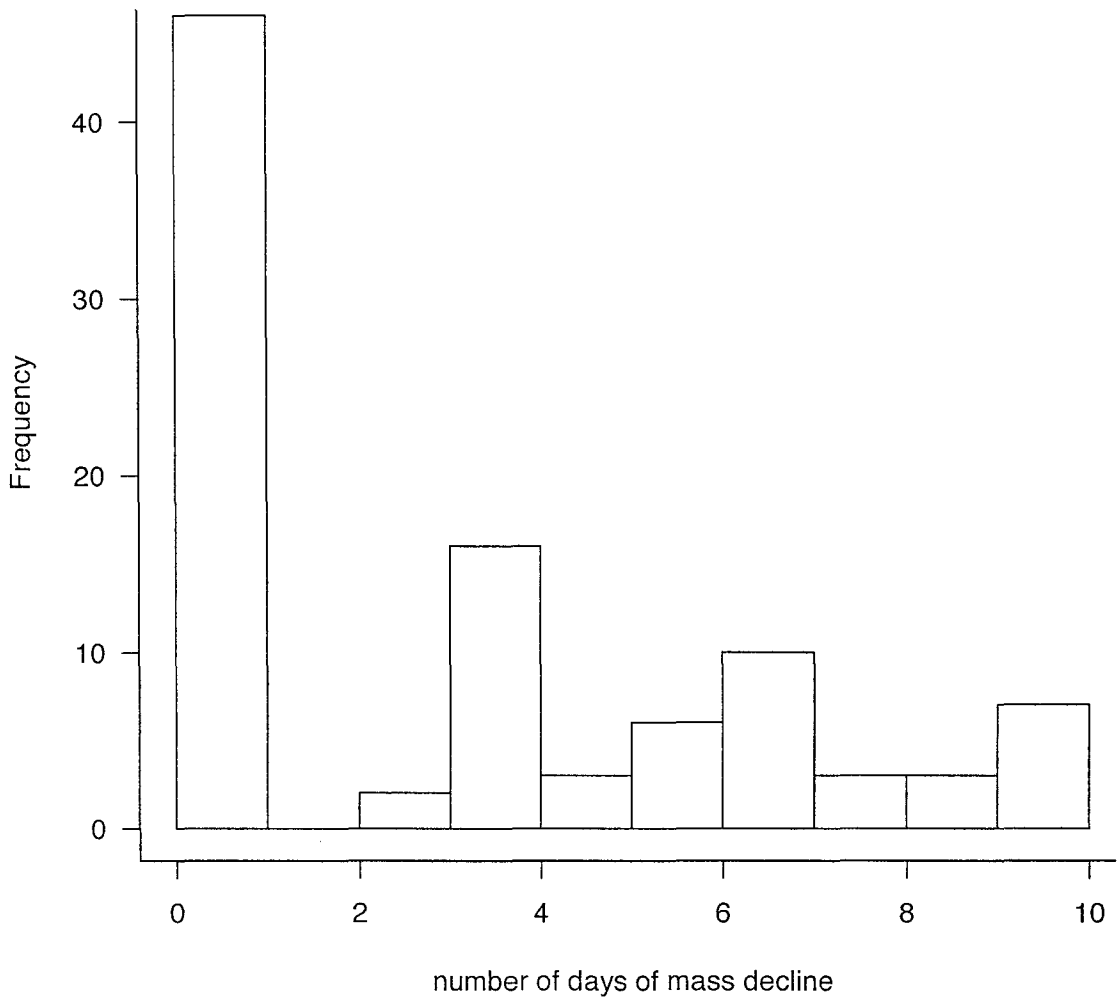

Figure 3.8 Frequency and length of pre-fledging mass decline in Least Auklet (*Aethia pusilla*).

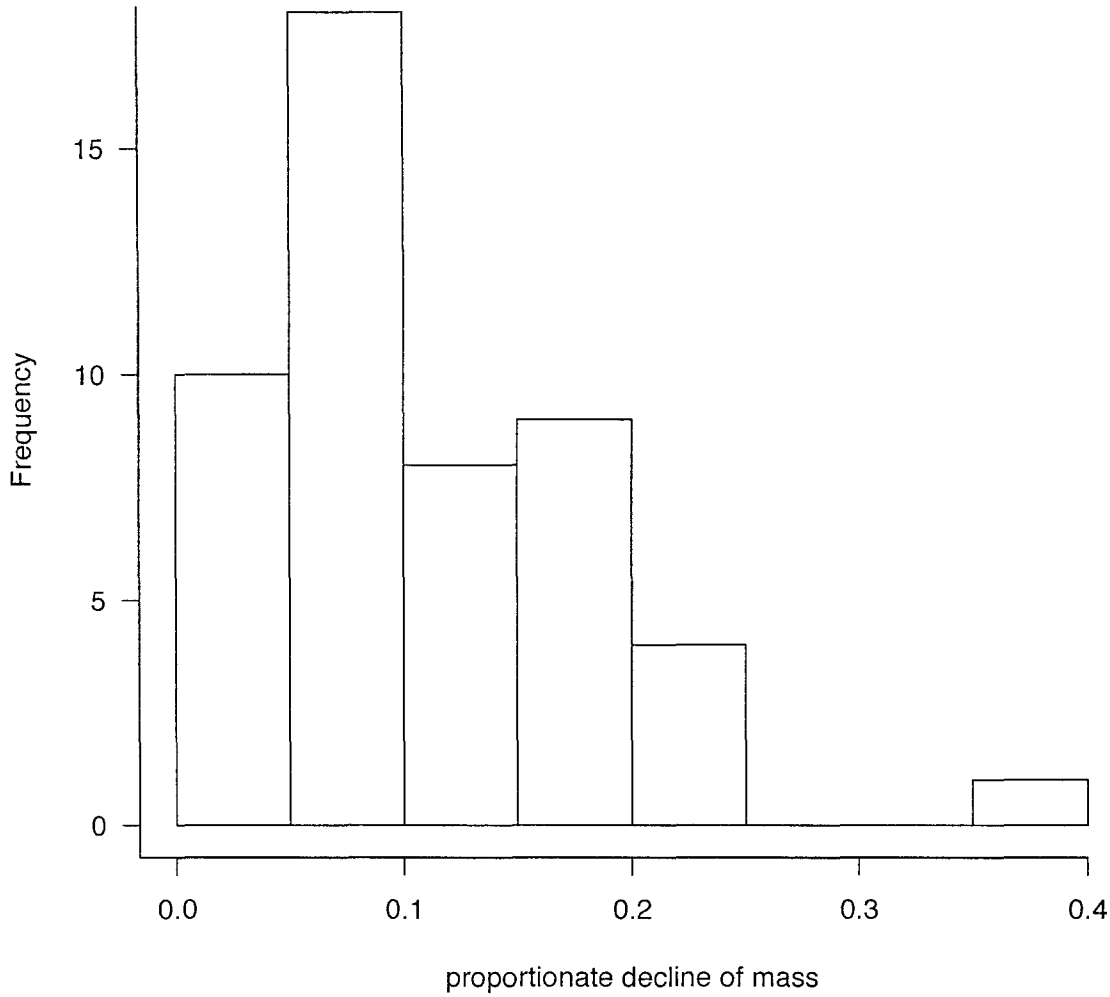

Figure 3.9 Mass loss as a proportion of maximal mass in those chicks that showed pre-fledging mass loss. Because we had to use only two data points, rather than a fitted function, to estimate mass loss, daily fluctuation in chick mass and measurement error can distort this pattern considerably (e.g. the bird which appears to have lost over 40% of its peak mass).

Table 3.4 Summary statistics of measurements of breeding Least Auklet adults caught in the crevice.

	mean	se	CV	N	min	max
mass	83.0	0.3892	6.53 %	194	66.8	102
head+bill	42.6	0.0793	2.60 %	196	40	46
wing	100	0.1738	2.43 %	196	93	106
tarsus	18.7	0.0545	4.07 %	196	16.7	21.1

Inter-annual variation

Inter-annual variation of all productivity and growth parameters is summarized in Table 3.5. Compared to within-year variation, inter-annual variation was greatest in the maximum growth rate of wing, the age of maximum wing growth, maximum growth rate of tarsus, and the fledging size of head+bill (in all these cases, there was statistically significant inter-annual variation). Chick survival (and productivity) were highest in 2002, while the length of the brooding phase was shortest in that year. Chick tarsus showed the fastest maximum growth rate in 2002 but the slowest wing growth rate and the latest age of maximum growth. Compared to the absolute size of a measure, fledging mass varied more among years than fledging size of any morphometric measurement, as indicated by the inter-annual CV.

Table 3.5 Inter-annual variation of breeding and chick growth parameters. Presented are the overall, unweighted mean, the means for each year, the coefficient of variation of the means between years, and a significance test of the inter-annual variation (ANOVA). All lengths are in mm, times are in days. Growth parameters tabulated are fledging size (FS), maximal growth rate (maxm), and time of inflection of the growth curve (t_0).

	mean	2000	2001	2002	CV	F	df	P	
Julian hatch date	178.6	178.2	178.2	179.8		1.175	91	0.281	
hatching success	0.843	0.905	0.813	0.821					*
chick survival	0.608	0.505	0.539	0.743					*
productivity	0.513	0.457	0.439	0.610					*
brooding length	4.5	5.1	4.2	4.0	12.5 %	1.92	61	0.171	
mass FS	81.3	90.3	74.1	81.0	9.9 %	3.11	89	0.081	
mass maxm	4.8	5.5	4.2	4.7	14.0 %	4.46	89	0.037	
mass t_0	12.2	12.1	12.0	12.3	1.2 %	0.09	90	0.770	
head+bill FS	39.3	40.5	38.4	39.2	2.7 %	5.78	89	0.018	*
head+bill maxm	4.4	5.2	4.0	4.3	14.0 %	1.10	89	0.296	
head+bill t_0	-2.5	-2.0	-4.5	-1.5	-59.8 %	0.93	89	0.336	
tarsus FS	18.7	18.7	18.7	18.8	0.5 %	0.47	58	0.497	
tarsus maxm	2.9	2.3	1.7	4.0	44.5 %	6.12	58	0.016	*
tarsus t_0	-7.8	-7.3	-11.1	-5.6	-35.3 %	0.59	58	0.446	
wing FS	86.4	86.6	85.0	87.3	1.3 %	0.35	89	0.553	
wing maxm	3.7	4.0	3.7	3.6	5.9 %	8.93	89	0.004	*
wing t_0	16.6	15.2	16.3	17.4	6.7 %	7.73	89	0.007	*

Testing the Ydenberg et al. (1995) model

We tested the predictions of Ydenberg *et al.'s* (1995) model in four separate linear models involving growth rate, fledging age, fledging mass, and hatch date with year as a covariate. In no case was the interaction term significant, so we omitted it. As predicted by the model we found a statistically significant negative relationship between hatch date and fledging age as well as fledging mass, and a positive relationship between fledging mass and maximal mass growth rate (Table 3.6). We did not, however, find the predicted negative relationship between fledging age and maximal mass growth rate (Figure 3.10).

Table 3.6 Test the prediction of Ydenberg *et al.* (1995) model on Least Auklet fledglings from Buldir Island. The model predicts that faster growing chicks fledge younger and heavier than slow growing chicks and that later-hatched chicks fledge younger and lighter than earlier hatched ones. All models include the factor "year" as a covariate.

model	estimate	F	df	P	supported
fledge age~growth rate	0.195	0.009	1, 87	0.9230	-
fledge mass~growth rate	4.019	17.727	1, 87	0.0001	++
fledge age~hatch date	-0.354	15.762	1, 92	0.0001	++
fledge mass~hatch date	-0.668	6.367	1 ,87	0.0134	++

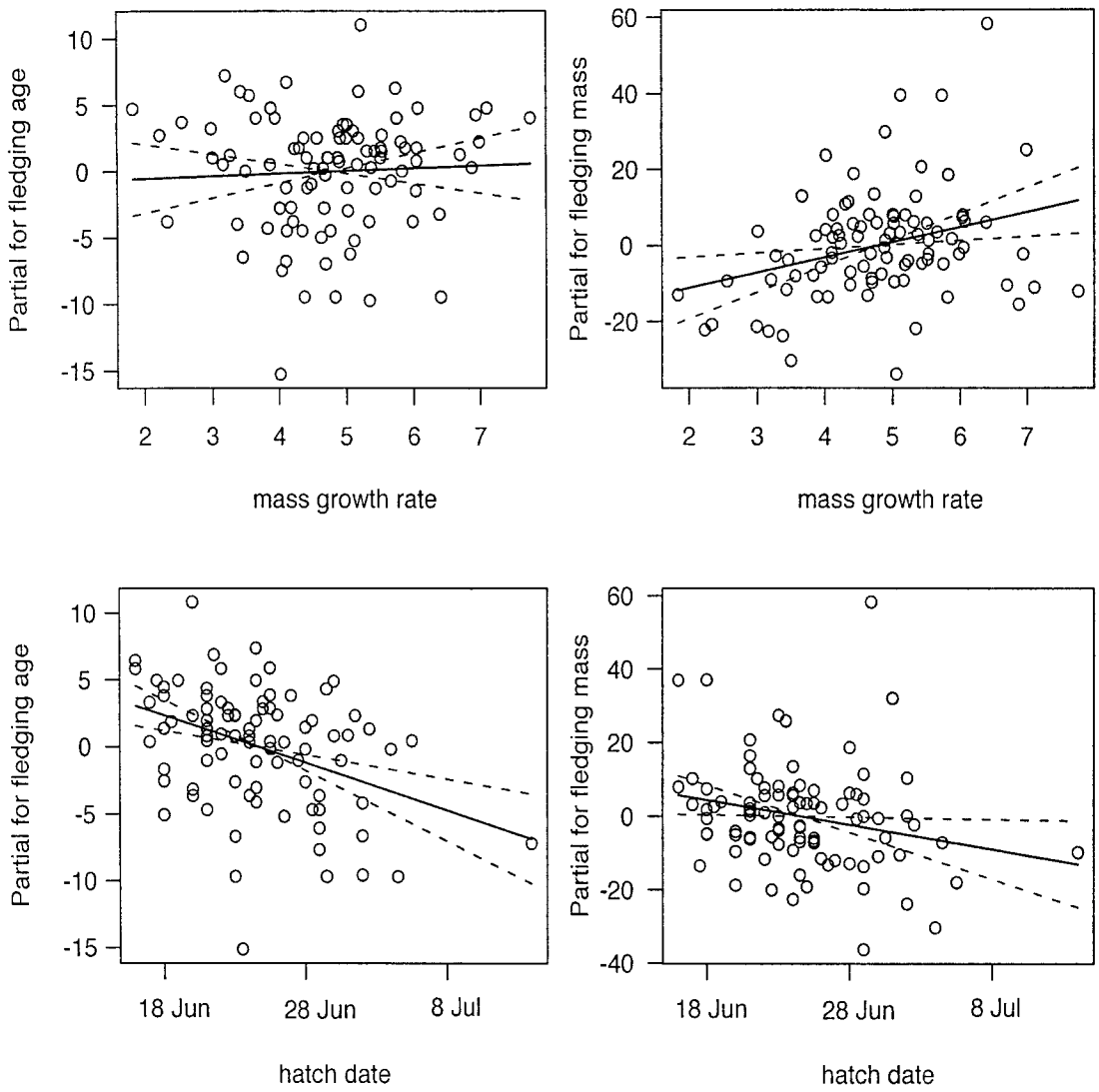

Figure 3.10 Test of Ydenberg *et al.* (1995) model. We included a factor "year" in the models to correct for differences among years. Plotted are the regression terms against their predictors with standard errors and partial residuals. The model predicts positive relationships of mass growth rate with fledging age and fledging mass, and negative relationships for between hatch date with fledging age and fledging mass.

Discussion

We quantified parameters of the breeding biology of Least Auklets during three years on Buldir Island in the western Aleutians. In contrast to colonies further north (Sealy 1975), late snow melt was never an issue for auklets breeding at Buldir Main Talus and hatching success was correspondingly consistently high. Most hatching failures were recorded after the mean hatching date (Figure 3.3), suggesting that adults were incubating infertile or otherwise addled eggs for a specific time beyond expected hatching before abandonment. The clutches hatching extremely late in 2001 and 2002 might have resulted from adults that lost their first egg and then relayed within the same season, as reported in rare instances in this species (Piatt *et al.* 1990) - but we never saw any incontrovertible evidence of relaying.

Breeding success

Estimating hatching success is notoriously difficult; in crevice nesting seabirds the task is particularly challenging. The Mayfield method is designed to account for breeding sites that have failed before being discovered; however, it relies on a constant mortality rate over time. In our study, Least Auklet eggs showed a fairly uniform, low mortality rate throughout the first 30 days incubation, corresponding to the normal incubation period reported for this species. A sharp increase in egg failure-events was observed afterwards, when eggs were expected to have hatched already. This pattern differs markedly from the constant mortality rate demanded by the Mayfield method and commonly found in terrestrial species (Johnson 1979). In the present situation, apparent

hatching success is probably the best estimate (Johnson, and Shaffer 1990). On other islands, where rodent predation is common (Piatt *et al.* 1990), the Mayfield method might be more appropriate. The difference between apparent and Mayfield estimates in this study was similar to that reported on St. Lawrence Island (Piatt *et al.* 1990), where vole predation occurred. While the two methods provided similar answers, we encountered problems when bootstrapping the Mayfield estimator to obtain standard errors (unrealistic extremes), which were likely a consequence of the unusual hazard function.

Crested Auklets can compete with Least Auklets for the same crevice and will displace them and damage or destroy eggs. Whiskered Auklet and storm-petrels have only a slight size advantage (the latter being actually lighter than Least Auklets), probably insufficient too compete aggressively with Least Auklets. While also present, Parakeet Auklets are too rare on Main Talus to show a noticeable impact on Least Auklets. The timing of egg failure (Figure 3.3) suggested that most failure related to infertile or addled eggs. Infertility or early embryonic failure was also found to be the main cause of hatching failure on Buldir in Knudson and Byrd's (1982) study.

Fledging success and productivity

Our productivity estimates were similar the estimate for an undisturbed control section on St. Lawrence Island, but significantly higher than productivity in an intensively monitored sector (Piatt *et al.* 1990). On St. George Island, breeding success was higher in the early 1980s (0.66 and 0.72, Roby, and Brink 1986) than reported either from St. Lawrence or in any year during this study.

Chick growth

Of all measurements taken, tarsus reached full adult size particularly quickly. This early growth allows the chick to be mobile from an early age and might help avoiding predation by congeners or puffins. This early growth made it difficult to establish maximal growth rate and t_0 for tarsus accurately, because the main growth burst often occurred during brooding and then missed. Estimates of maximal growth rate and age of maximal growth as presented here, are therefore not reliable. The high values for the CV of tarsal growth are especially likely to reflect a large measurement error relative to observed growth, rather than biological variation.

Several morphometric growth parameters showed significant inter-annual variation, but none of the mass growth parameters varied significantly between years. This is contrary to what we expected. In Little Penguins (*Eudyptula minor*), chick mass growth differed among years but not growth of flipper or tarsus (Renner 1998). The pattern of fledging sizes was similar to that found in Crested Auklet (Fraser *et al.* 1999), with wing length having the smallest fledging to adult size ratio.

On St. George Island, Least Auklet chicks grew at a similar rate to chicks on Buldir, but asymptotic mass was about 26 % greater than on Buldir (Roby, and Brink 1986). The brooding phase was longer on St. George (6 days compared to 4.5 days on Buldir), but fledging age did not-differ appreciably between the two islands (28.6 days on St. George, 29.1 days on Buldir). In contrast to Buldir, Least Auklets on St. George did not go through a period of pre-fledging mass recession. Mass recession of about 5 g has been reported for Least Auklets on St. Lawrence Island (Sealy 1973), but was more extreme on

Buldir Island. In Dovekies, this mass loss was associated with a lack of provisioning by the female parent, rather than a reduction in feeding frequency by both parents (Harding *et al.* 2004). In contrast to auklets, Dovekie males continue provisioning their chicks at sea after fledging (Gaston, and Jones 1998). In Crested Auklets it is the male that provides less frequently for the chick (Fraser *et al.* 2002) - whether reduced provisioning by one parent is responsible for the decline in Least Auklet chick mass on Buldir remains to be seen.

Ydenberg et al. model

As in many other alcids (Ydenberg 1989), but unlike Crested Auklets (Fraser *et al.* 1999), we found negative relationships of hatch date with fledging mass and fledging age. We did not, however, find the predicted negative relationships of growth rate with fledging age and fledging mass. The observed recession of mass prior to fledging is a further indicator that mass was likely not the trigger for fledging. Wing length, on the other hand, showed maximal growth at a later age and still displayed a smaller CV in fledging size (Table 3.3). This indicates, as suggested by Hipfner and Gaston (1999) for Thick-billed Murre (*Uria lomvia*) and Razorbill (*Alca torda*), that wing length, rather than mass, triggers fledging. The observation at Buldir that most successful fledglings involved the departing juvenile flying strongly from the breeding crevice entrance to the sea (MR and ILJ, pers. observ.) underlines the survival advantage of complete wing development.

Variation in breeding biology among the alcids and selection for small size

The Least Auklet is the smallest member of the family Alcidae. Virtually all members in the sibling family Laridae (Sibley, and Ahlquist 1990) are considerably larger, making it very likely that the small size of Least Auklets is a derived character of the species rather than a plesiomorphic character. Within the auklets, Cassin's Auklet is basal to all other auklet species, whose relationships have not been resolved (Friesen *et al.* 1996). The basal position of Cassin's Auklet with Least Auklet nested within the auklet tree shows that Least Auklet's small size is a derived trait. While there is ample evidence for selection favouring large size, little is known about the evolution of small size (Blanckenhorn 2000). Amongst the alcids, Least Auklet chicks fledge (leave the breeding site) at an unusually advanced developmental stage after the shortest nestling period of any semi-precocial alcid (Figure 3.11). In most alcids fledging marks a transition where adults change from bringing food to the chick to bringing the chick to the food. The latter stage was suggested to be energetically favourable to the adults but to poses greater mortality risk for the chick (Ydenberg 1989). Only Black Guillemot (*Cepphus grylle*) and Pigeon Guillemot (*C. columba*) raise their chicks to almost full adult mass in the nest as well (Cairns 1981; Emms, and Verbeek 1991). Compared to other alcids, guillemots forage very close inshore. Frequent visits to the nest are therefore less energetically costly and time consuming than for species that have to travel tens of kilometres or more to reach the nest from the foraging area.

So what factors led Least Auklets to evolve a small size? We presume that Least Auklets evolved from an ancestor that provisioned its chick and was generally diurnally active at breeding colonies. Adult Least Auklets are active only in daylight and suffer depredation by raptors, gulls, and mammalian predators (Gaston, and Jones 1998). In this high risk (to adulthood) situation, individuals that made fewer provisioning trips to the colony site would be favoured, making rapidly growing chicks and relatively large chick meals advantageous. Least Auklets appear to possess a suite of characteristics that help meet this challenge. Although only a tenth the size of the largest alcid, Least Auklets deliver chick meals up to 10 g (mean = 5.4 g) on average 5.3 times per day (Roby, and Brink 1986), likely made possible because of the load bearing advantages of small body size. Furthermore, Least Auklets' small size likely provides foraging advantages compared to larger species. Most small auks feed on small zooplankton that are collected individually (Gaston, and Jones 1998). Least Auklets prey extensively on Calanoid copepods (Jones 1993), which are abundant, rich in lipids, and available near the surface, but very small compared with the average zooplankton preyed upon by other seabirds. Small size must convey advantages to a species specialized on the smallest zooplankton since each prey item will be larger in proportion to the birds' own body mass. Additionally, having a smaller body size would require a Least Auklet to bring fewer food items to their chick than congeners to grow by similar proportion to full development. This would allow them to stay longer in the crevice and to reach a more advanced developmental state before being exposed to the increased mortality hazard at sea.

Within the monophyletic group of puffins and auklets (Friesen *et al.* 1996), Least Auklets are at an extreme in mass, proportionate fledging mass, and fledging age (Figure 3.11). There appears to be a strong negative relationship between adult body mass and the relative fledging mass of the chick and a positive relationship between adult mass and fledging age. This observation supports the notion that the evolution of rapid and advanced chick development has been intricately linked with the evolution of small size in this group.

Our study clarifies the breeding biology of the Least Auklet, in which diurnal colony attendance and specialization on a copepod diet have combined to favour small adult body size and rapid offspring development. Further research on this species needs to be directed at causes of annual variation in reproductive success and particularly winter ecology. The species' range, movements, diet and causes of mortality during winter are virtually unknown, even though it is one of the most abundant North Pacific seabirds.

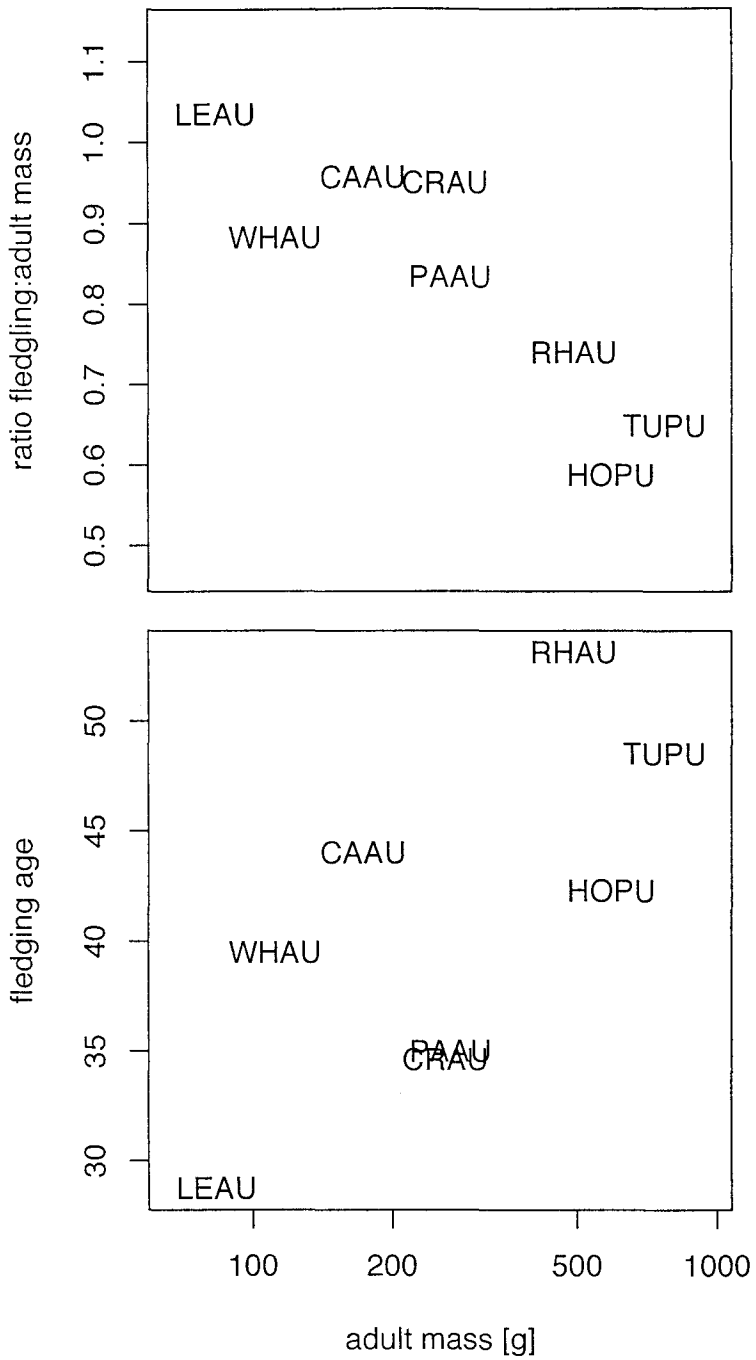

Figure 3.11 Comparison of fledging age and the relative fledging mass to adult mass (on a log scale) in auklets and puffins. The species presented are *Ptychoramphus aleuticus* (CAAU), *Aethia cristatella* (CRAU), *Fratercula corniculata* (HOPU), *Aethia pusilla* (LEAU), *Aethia psittacula* (PAAU), *Cerorhinca monocerata* (RHAU), *Fratercula cirrhata* (TUPU), and *Aethia pygmaea* (WHAU). Note that the three nocturnal species here (WHAU, CAAU, RHAU) fledge late for their size. Data from (Harfenist 1995; Gaston, and Jones 1998 and sources within; Fraser *et al.* 1999; Jones *et al.* 2001; Hunter *et al.* 2002; Piatt, and Kitaysky 2002).

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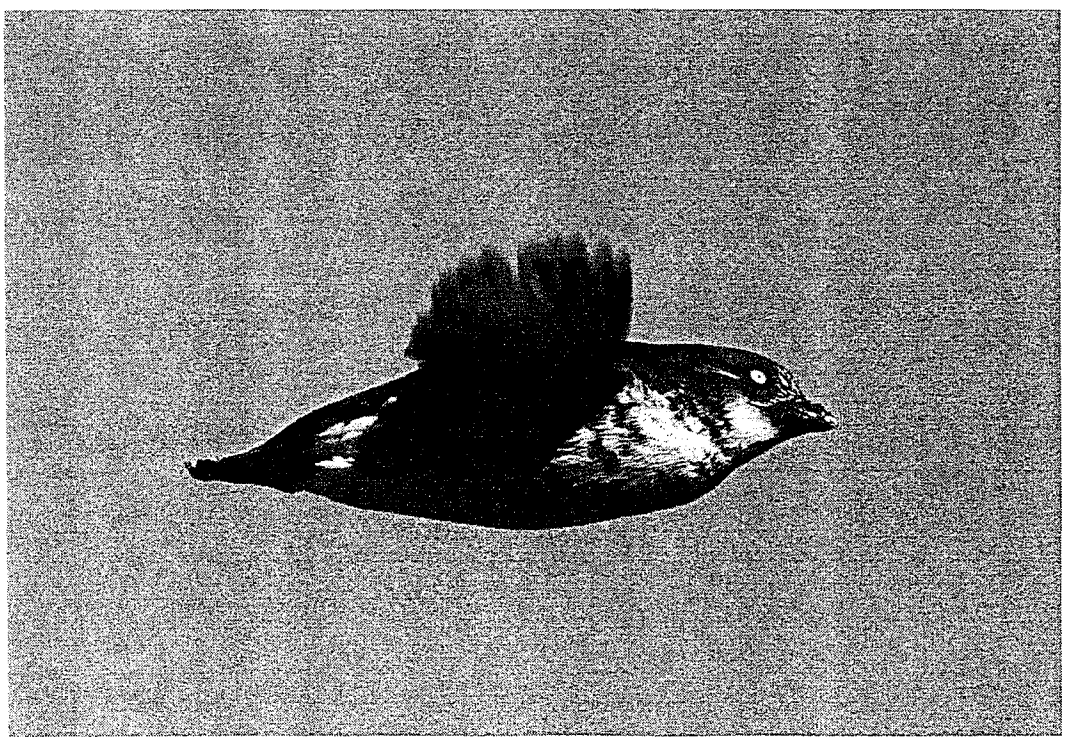
Chapter 4.

Repeatable measures of take-off flight performance in auklets

M. Renner



Abstract

Rapid acceleration is the key to a successful escape manoeuvre. It has attracted considerable research attention in a wide array of taxa. I recorded take-offs of Least Auklet (*Aethia pusilla*) and Crested Auklet (*Aethia cristatella*) with digital video (60 f/s). To smooth time-location data derived from video, I used predicted mean square error quintic splines, which have been shown to be good predictors of true acceleration. Repeated recordings of the same individual bird allowed me to measure repeatability of take-off acceleration and velocity to find the most robust and biologically meaningful measure. The most repeatable take-off parameters were power at t = 0.17 s (r = 75 %), and acceleration at t = 0.17 s (r = 72 %). The horizontal component of velocity at t = 0.32 s was least affected by the slope of the take-off trajectory. Mean acceleration of both species is close to expected values based on body mass. Within Least Auklets, however, I did not find a significant relationship of velocity or acceleration with mass. A relationship would be if the observed drop in body mass of breeding adults after hatching is an adaptation to reduce the risk of predation. After adjusting for differences in air density, the acceleration values found here for Least and Crested Auklets fit closely the power-function of acceleration in dependence of log (mass) previously reported, despite having considerably greater mass than the species for which this function had been previously reported. I conclude that velocity at a certain time after take-off is repeatable and the most suitable measure of performance for both inter- and intra-specific comparisons.

Introduction

Rapid escape behaviour is often the only way an animal can avoid becoming prey. Rapid acceleration is also vital for many predators to capture their prey, (e.g., Harper, and Blake 1991; Tucker *et al.* 1998). Considering this fundamental importance in predator-prey interactions, it is not surprising that the study of rapid escapes, fast-starts, or take-offs has become an active field of research. Escape behaviours and accelerations have been quantified in a wide range of taxa, including crustaceans, insects, molluscs, teleosts, amphibians, and birds (Brackenbury 1991a, b; Sunada *et al.* 1993; Cheng *et al.* 1996; Lee *et al.* 1996; Domenici, and Blake 1997; Vogel 1997; Lind *et al.* 1999; Nauen, and Shadwick 1999; Navas *et al.* 1999; Kullberg *et al.* 2000; Burns, and Ydenberg 2002; Burrows, and Morris 2002; Tytell, and Lauder 2002). In particular maximum acceleration has been of interest as a measure of performance.

Fast starts and take-offs are of particular relevance to functional biology, kinematics, and behavioural ecology. While there is a great need for accurate measurements of acceleration, obtaining them is a different matter. It is most convenient, and popular, to estimate acceleration from frame-by-frame analysis of video as the second derivative of location with respect to time. Unfortunately, small measurement errors, especially when using high frame-rates, create noisy and exaggerated estimates of acceleration. Smoothing can remove the noise but it also flattens a peak. This led Harper and Blacke (1989) to the conclusion that high-speed video is inherently unsuitable for estimates of instantaneous acceleration. However, Walker (1998) showed that predicted

mean square error (MSE) quintic splines (Woltring 1986a) perform remarkably well when compared to known acceleration profiles.

Given the difficulties and many potential sources of error of measuring acceleration and velocities from video data, it is important to scrutinize the precision of measurements of velocity and acceleration. Without testing precision it is impossible to interpret any negative results, i.e. any failure to detect an effect could be the result of an existing effect being masked by a large measurement error. Acceleration can be measured directly using implanted accelerometers (Harper, and Blake 1990, 1991; Yoda *et al.* 1999, 2001). While this is the preferred method for measuring acceleration, there are also serious drawbacks, such as size and weight of the device, which are prohibitive for many smaller species. Also, use of data loggers requires that the animal be recaptured later, which can be difficult.

Because it was not practical to measure accuracy directly, I calculated repeatability of take-off speed and acceleration. Repeatability is the proportion of the overall variance in a character that occurs among rather than within individuals, and can also be interpreted as the within-class correlation coefficient (Falconer 1981; Lessells, and Boag 1987; Sokal, and Rohlf 1995; Zar 1996). For example, a 75 % repeatability would mean that three quarters of the observed variance is due to inter-individual variance, and the remaining quarter is due to within-individual variance. Commonly used in morphometric studies, repeatability is a way of assessing precision and measurement error. Because every take-off is a unique event, it was not practical to apply repeatability in the traditional sense in which the same unit is measured repeatedly. Instead, I use

repeatability to compare repeated take-offs of the same individual on different days with take-offs of other individuals. Values of repeatability reported here will therefore be based on within individual variance and variance due to measurement error, leading to smaller values of repeatability than calculations based on measurement error alone. At > 50 % repeatability, among individual variance is larger than within individual variance, broadening the versatility of take-off measurements for addressing questions about predator-prey interactions to more general questions of recognising individual quality. Repeatability is commonly been applied to measures of performance in fish, amphibians, and reptiles (see Kolok 1999 for a review), but only one study applies this measure to mechanical performance in birds (Bonser, and Rayner 1996).

Out of the many possible parameters to measure during a take-off (e.g., time to cover a certain distance, velocity after a set time, maximum acceleration), it is often unclear which would be the most suitable and robust parameter for the question at hand. Matters are further complicated by birds that fly in trajectories of variable slope, making differential use of gravity to aid or slow acceleration. Different researchers have chosen different measures based on experimental conditions or perhaps intuition, but so far, no study using take-off performance as an ecological indicator has made an effort to compare these different parameters and select the most suitable. In this paper I will use repeatability to select amongst several measures of take-off performance, including force and power, and assess how to deal with trajectories taking different slopes.

I quantified take-off parameters for two auklet species (*Aethia pusilla* and *A. cristatella*) and compared the most suitable measure with the bird's mass, wing length

and wing loading. Breeding auklets, like many other birds, undergo a decline in mass after their clutch hatches (Jones 1994; Gaston, and Jones 1998). It has been debated whether this decline in mass is due to the increased energy demand of rearing chicks or an adaptive reduction in adipose tissue (programmed mass loss hypothesis) to reduce the cost of flight (Freed 1981; Jones 1994; Kullberg *et al.* 2002a,b). A lighter bird will not only expend less energy when flying, it might also experience a lower predation risk through increased flying capabilities (Gosler *et al.* 1995). I tested the hypothesis that a bird profits from maintaining a lower body by examining the relationship between acceleration and body mass.

Materials and methods

Study species and site

The Least Auklet (*Aethia pusilla*) is a small, 81.5 g (mean in this sample), seabird with short wings (aspect ratio 7.3), a wing loading of 71 N m^{-2} and the smallest wing area of any seabird (Spear, and Ainley 1997). Least Auklets are constrained by high wing loading and high energetic costs of flight due to adaptations for both flight in air and wing-propelled locomotion underwater (Roby, and Ricklefs 1986). The species breeds in a few large colonies throughout the Bering Sea and Sea of Okhotsk where it is likely the most abundant seabird (Jones 1993; Stephensen, and Irons 2003). At 257.3 g (mean in this sample), Crested Auklet (*Aethia cristatella*) are considerably larger than Least Auklets with which they often breed in mixed colonies. Wing loading (97 N m^{-2}) and aspect ratio (8.2) are slightly higher than in Least Auklet. Avian predators, such as

Peregrine Falcons (*Falco peregrinus*), Bald Eagles (*Haliaeetus leucocephalus*), Glaucous-winged Gulls (*Larus glaucescens*), Glaucous Gulls (*L. hyperboreus*), and Common Ravens (*Corvus corax*) pose a constant threat at many colonies (Jones 1993). Naturally occurring mammalian predators are absent from many auklet colonies, making avian predators usually the only threat auklets encounter on land. Fast acceleration on take-off therefore may be an important factor to the survival of auklets.

This study was conducted on Buldir Island (52°21'N 175°56'E) during May-August 2001 and 2002. Mean air temperature was 10°C (with extremes at 3°C and 19°C), mean air pressure at sea level was 1008.8 hPa. Take-off trails were conducted within the colony, 80 m above sea level. Relative humidity was high, usually between 80 and 90 %. The predicted air density from these values is 1.249 kg/m^{-3} (102 % of standard air density). Lower temperature, and elevation and probably higher humidity as well, mean that air density was likely to be 10 to 20 % denser than encountered by DeJong (1983) and Warrick (1998), who measured take-off acceleration in Wisconsin and Montana, respectively. Because air density is linearly related to air foil performance (Pennycuick 1989), flight performance can be expected to be 10 to 20 % greater, too.

Experimental procedure

Auklets were captured on the ground by their feet with monofilament nooses during the morning activity period (Byrd *et al.* 1983; Jones 1993). Birds were weighed, measured, blood sampled by vein puncture for sexing, and held in canvas bags for up to 1 1/2 hours until release. Just before release, birds were held by hand facing down-slope on a horizontal wooden plank on my study plot about 80 m above sea level. They had a

clear view of their surroundings, the ocean, and the horizon. Take-offs were recorded using a Sony DCR-TRV 525 (NTSC) digital camcorder placed 3 m to one side of the take-off platform with the optical axis perpendicular to the anticipated flight trajectory. Four plastic flags were placed below the trajectory to determine whether the bird took off at an angle perpendicular to the camera (Figure 4.1). An assistant positioned behind the bird recorded which flags the bird's trajectory fell between and also acted as an artificial predator to flush the auklet with a quickly raised hand movement, should the bird hesitate to fly off immediately after being released from the hand. Differences in motivation could have resulted in differences in effort and take-off performance. Because all birds were handled immediately before release, I believe that every bird tried to escape what appeared to be a life-threatening situation. Temporary disorientation from the stress of handling could have been the cause of hesitation in some birds. Most take-off trials were conducted in calm wind conditions. Local crosswinds up to 1 ms^{-1} were considered acceptable. Beyond that, or during perceptible head/tailwinds, trials were aborted. Wind speeds were checked by timing a falling down feather over a distance of 2 m.

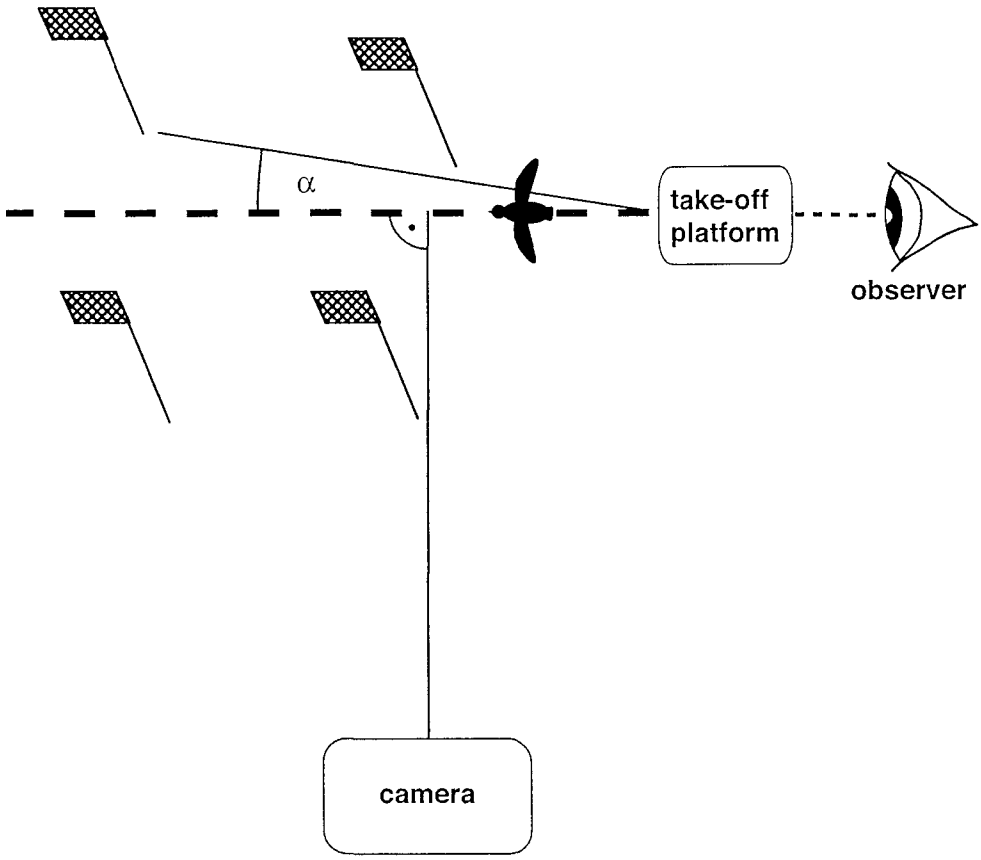


Figure 4.1 Bird's eye view of the experimental set-up showing the take-off platform, video camera, and the bird's trajectory. Plastic flags were placed underneath the flight-path to estimate the angle α between the bird's trajectory and the ideal trajectory perpendicular to the camera.

Video analysis

Digital video was transferred via Firewire™ connection to a hard drive and saved as QuickTime™ files in native digital video (DV) format. NTSC format is interlaced and records 29.97 full frames per second. An interlaced frame is made up of two halves

recorded sequentially, each containing only every other row of pixels necessary to build up the entire image. Using Deinterlacer 1.3 (Integrated Knowledge Systems 2000), both half-frames were preserved and the missing pixel rows reconstructed by interpolation, effectively doubling the frame rate to 59.94 frames/second.

The deinterlaced files were read into Adobe ImageReady (part of Adobe Photoshop 7.0) and a new layer created on which the horizon, a known distance as scale, and the position of the auklet's eye on every individual frame were marked. The first frame on which the bird had no more contact with the take-off platform was recorded as the beginning of the flight phase (t = 0). This new layer was saved as a GIF file and analysed using the public domain NIH Image 1.6.2 program (U.S. National Institutes of Health 2002). The image was calibrated and adjusted for the non-square pixel ratio of the NTSC format. Coordinates for the bird's position on every frame were saved and read into a database. The angle of the observed horizon to a vertical line in the image was used to adjust the coordinate system to the horizon. A correction was applied for acute/obtuse camera-to-trajectory angles (Figure 4.1). To avoid strongly non-linear effects, birds that took off at an angle > 20° from a line perpendicular to the camera axis were eliminated. Birds that didn't fly off, but just jumped/dropped down from the take-off pad, were also excluded. 274 take-offs of Least Auklets and 40 of Crested Auklets were left in the sample. MSE quintic splines (Craven, and Wahba 1979; Woltring 1985) require an *a priori* estimate of the error made during digitisation, which is used to adjust the degree of smoothing. The error variance (VAL) was calculated from five repeated digitisations of the same take-off sequence containing 31 frames. The average variance for repeated

measurements of the same frame was VAL = 1.53 cm^2. Many birds flew along a curved rather than a straight-line trajectory (Figure 4.2). To measure the distance along the trajectory two splines were fitted, one to the horizontal x and one to the vertical y coordinates. First and second derivatives of the splines with respect to time were then used to calculate velocity and acceleration, respectively, at 350 positions along the bird's flight path. Vector addition was used to construct velocity along the trajectory. Acceleration is comprised of two components: acceleration along the trajectory and perpendicular to it (change in direction). Acceleration along the trajectory was obtained by projecting the combined acceleration vector onto the velocity vector. For purposes of this paper I treat power (t) as the rate of change in kinetic energy, which should not be confused with a physiological measure of energy expended per unit time. Power (t) was calculated from mass * acceleration (t) * velocity (t).

When taking off, many birds, especially birds with high wing loading such as alcids, fly downwards and use gravity to aid acceleration to reach a velocity sufficient for level flight (Rüppell 1980). In this experiment, birds could choose their takeoff angle anywhere between +90° straight up to down the talus slope - which translates to an angle of about -45° (measured from a photo relative to the horizon). Birds could use gravity to a varying degree depending on the steepness of the slope they chose for the take-off trajectory. This could confound the search for a repeatable measure. If Θ is the angle between the horizon and the trajectory, $g \sin(\Theta)$ is the component of g available to the bird to add to its acceleration, and therefore I expect take-off acceleration to be proportional to $\sin(\Theta)$. $\Theta(t)$ can be read as a time-dependent variable from the $\tan^{-1}$ of the

slope of the velocity vector. I also calculated an average Θ over the flying phase from the ratios of the standard deviations of y and x. To compensate for the effect of slope, I added sin(Θ) as a covariate to linear models used to analyse acceleration or velocity. For maximum acceleration I used the sin(Θ) (t) at that particular time. For velocities and average acceleration I used the average sin(Θ). Unfortunately, there is no way of knowing *a priori* whether a bird will actually utilise gravity and turn it into forward motion, or whether a bird flying downwards does not yet produce enough lift to keep it in level flight. Therefore, I also analysed the horizontal component of acceleration separately.

Repeatability

Because take-offs of several individual Least Auklets were recorded on different days, it was possible to use repeatability *r* (Lessells, and Boag 1987) to compare the usefulness of different kinetic parameters. Since I did not have sufficient data for Crested Auklets, I based all calculations of repeatability on Least Auklets measured in the year 2002 only. The data were restricted to the year with most observations (2002) to avoid ambiguities over the appropriate sampling unit. 167 birds were recorded only once, 14 birds twice, 1 bird three times, and another bird four times. These numbers were used to calculate $n_0 = 1.104$ as needed for the calculation of repeatability *r* (Lessells, and Boag 1987). Since not all birds were observed for the entire length of flying time considered here, this number varied slightly over the time considered. I compared the repeatability of the following measures: maximum acceleration, average acceleration, trimmed average acceleration (central 50 %), and velocity at 351 moments evenly spaced in time between -

0.2 and 0.5 seconds after the bird lost contact with the take-off pad. Significance of repeatability of the measure y was tested as an ANOVA with the individual auklet as a random variable. The relatively small sample of 16 birds used to estimate within-individual variance should be kept in mind when interpreting, e.g., the shape of the function of repeatability over time may not be highly robust. Throughout this paper I report means ± SE. All statistical computations were performed in R 1.8.1 (Ihaka, and Gentleman 1996; R Development Core Team 2003) running under XDarwin on a G4 Apple PowerPC. Quintic splines were fitted with the FORTRAN program GCVSPL (Woltring 1986b).

Results

On Buldir Island, Peregrine Falcons and especially Glaucous-winged Gulls prey daily on auklets. Gulls usually fly at low levels over the colony and chase after flushed auklets. If an auklet is not caught within the first few meters of the chase, it might be pursued over the water.

After losing contact with the take-off pad, auklets chose a downward pointing trajectory (Figure 4.2) and began to fly down the talus slope like a bird would when chased by a gull or falcon. Average speed (t) and acceleration (t) profiles are shown in Figure 4.3. On average, birds increased their acceleration until they lost contact with the ground but were able to maintain a high acceleration for another 0.2 seconds. Average power (t) showed a steady increase until 0.2 seconds after take-off when it levelled off.

Individual velocity and acceleration profiles were much more variable, however (see appendix).

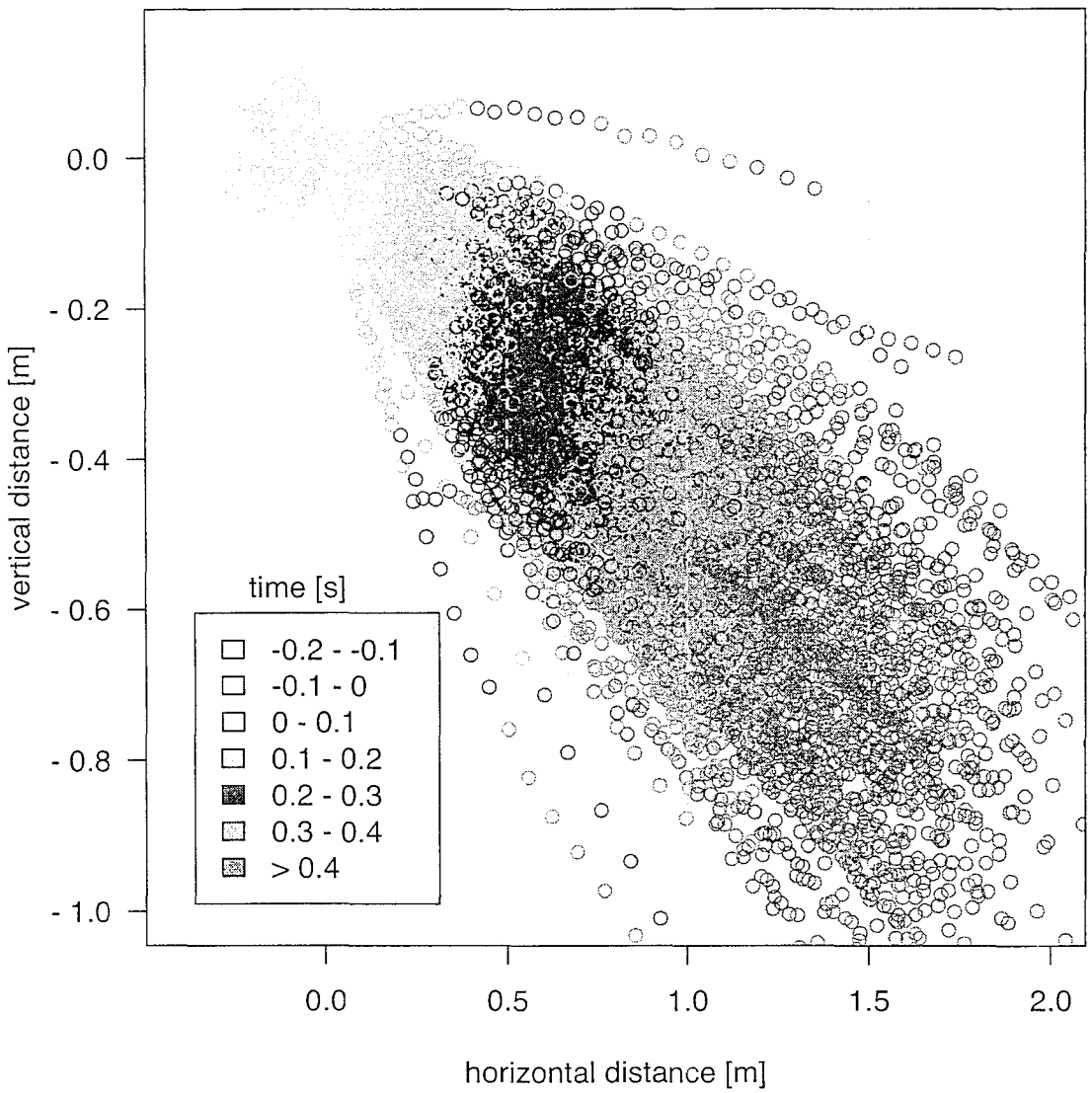


Figure 4.2 Trajectories of 274 Least and 40 Crested Auklet take-offs. The time t=0 is the first video frame where the bird had no more contact with the take-off platform. The vertical axis is stretched by a factor 2 compared to the horizontal, so take-offs slopes appear to have twice the true angle. Note that birds flying a steeper trajectory tend to be faster.

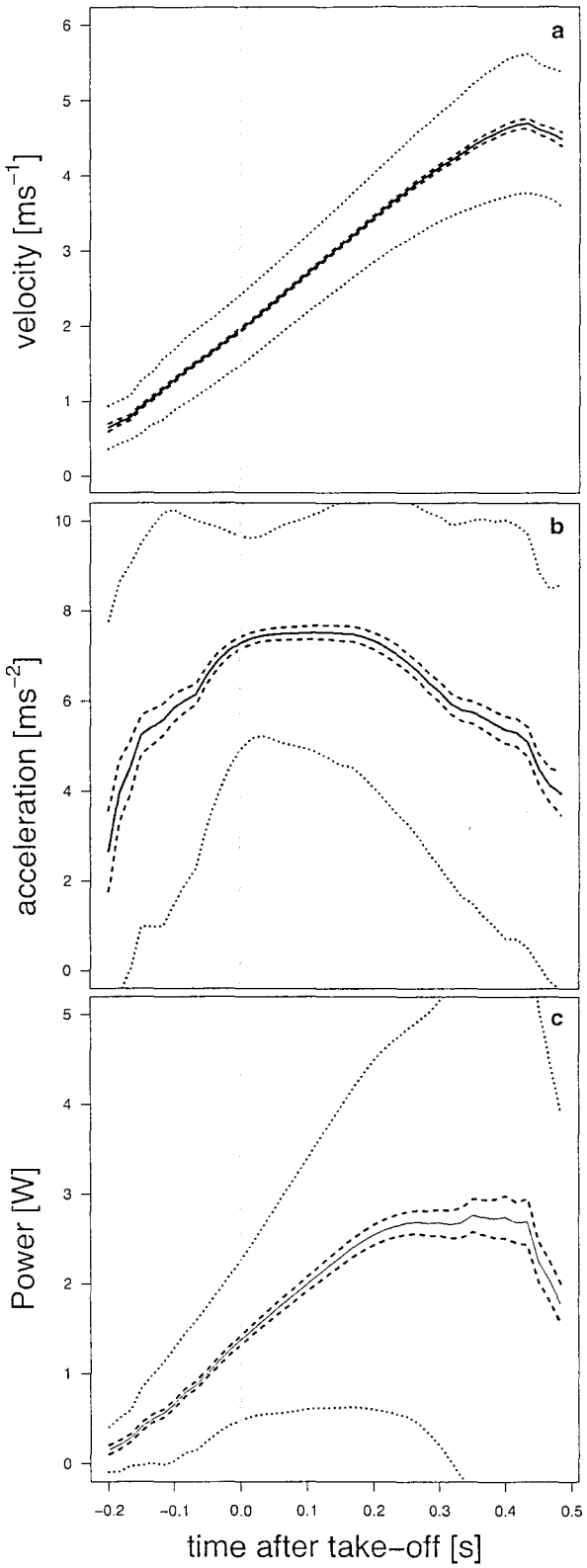


Figure 4.3 Velocity-time (a), acceleration-time (b), power-time (c) profiles (solid line: mean of individual fits, dashed: SE, dotted: SD). No corrections for differences in take-off slope are applied. Velocities and accelerations are derived from first and second derivatives of quintic splines fitted to time-location data, respectively. Horizontal and vertical location components were smoothed independently and then combined by vector addition. Power is calculated from acceleration, velocity, and mass.

Power at t = 0.17 s had the highest repeatability of all parameters (75 %), followed by acceleration at t = 0.17 s (72 %) (Table 4.1). Both times are the respective maxima of repeatability during take-off (Figure 4.4). The close relationship between repeated take-offs is further illustrated by plotting power and acceleration of the first take-off against a later take-off of the same bird (Figure 4.5). The coefficient of variation (CV) of acceleration was large compared to the CV of velocity or mass (7 %). For the sample considered, body mass had a repeatability of r = 0.21, resulting in power being largely a function of acceleration (r^2 = 0.87), rather than velocity (r^2 = 0.52) or mass (r^2 = 0.02). Repeatability of the slope of the trajectory was low (18 %), however, and only in one measure was repeatability greater when considering only movements along the horizontal x-axis. All take-off parameters investigated had a negative relationship with slope (downward slopes being negative). The relationship with slope was strongest in acceleration measured along the horizontal at t = 0.18 s (r^2 = 0.17). Least affected by slope was the horizontal component of velocity, measured at t = 0.32 s.

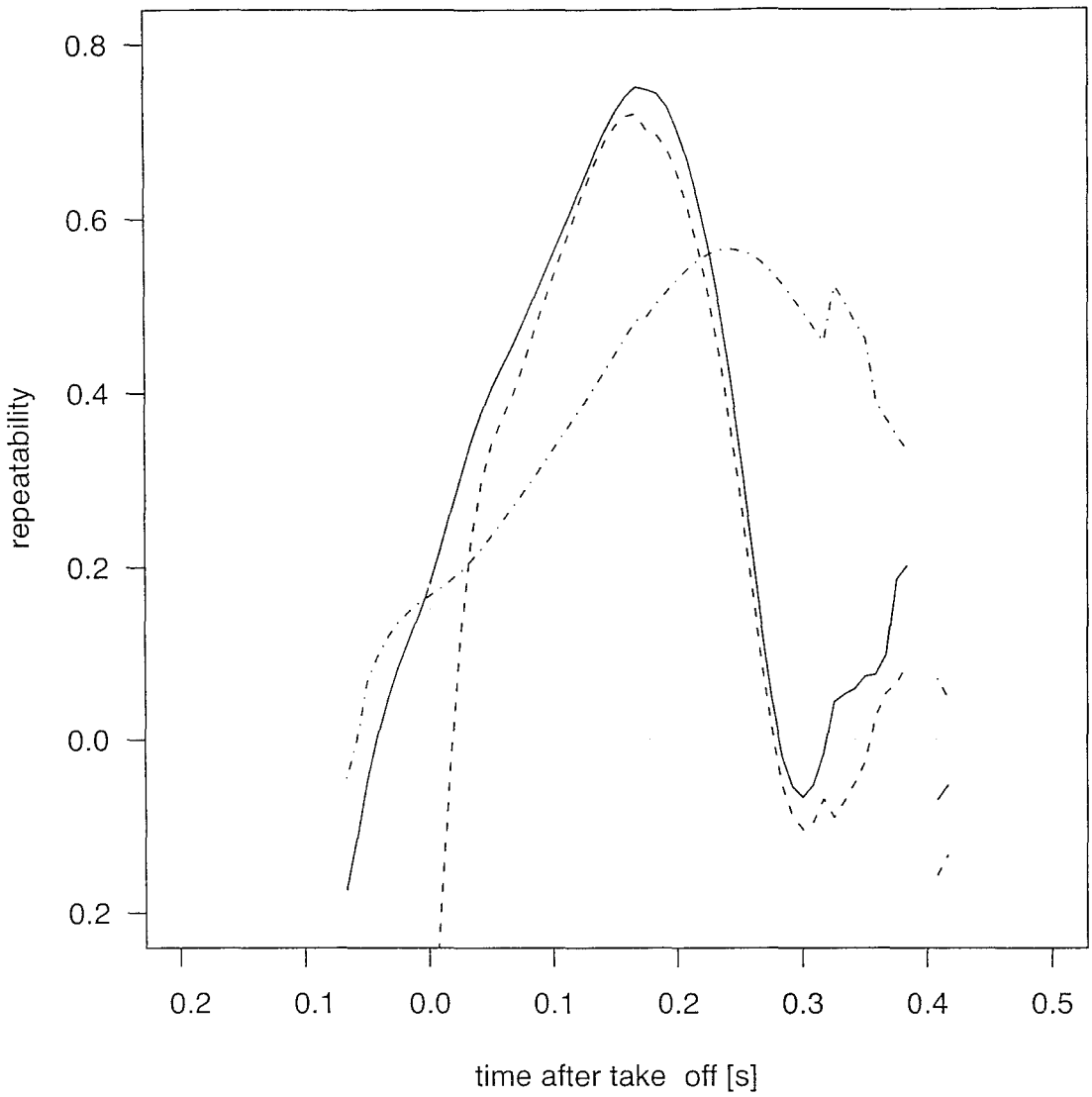


Figure 4.4 Repeatability (as measured by repeated measurements of the same individual) of velocity (dash-dot), acceleration (dashed) and power (solid) measures at time t after take-off.

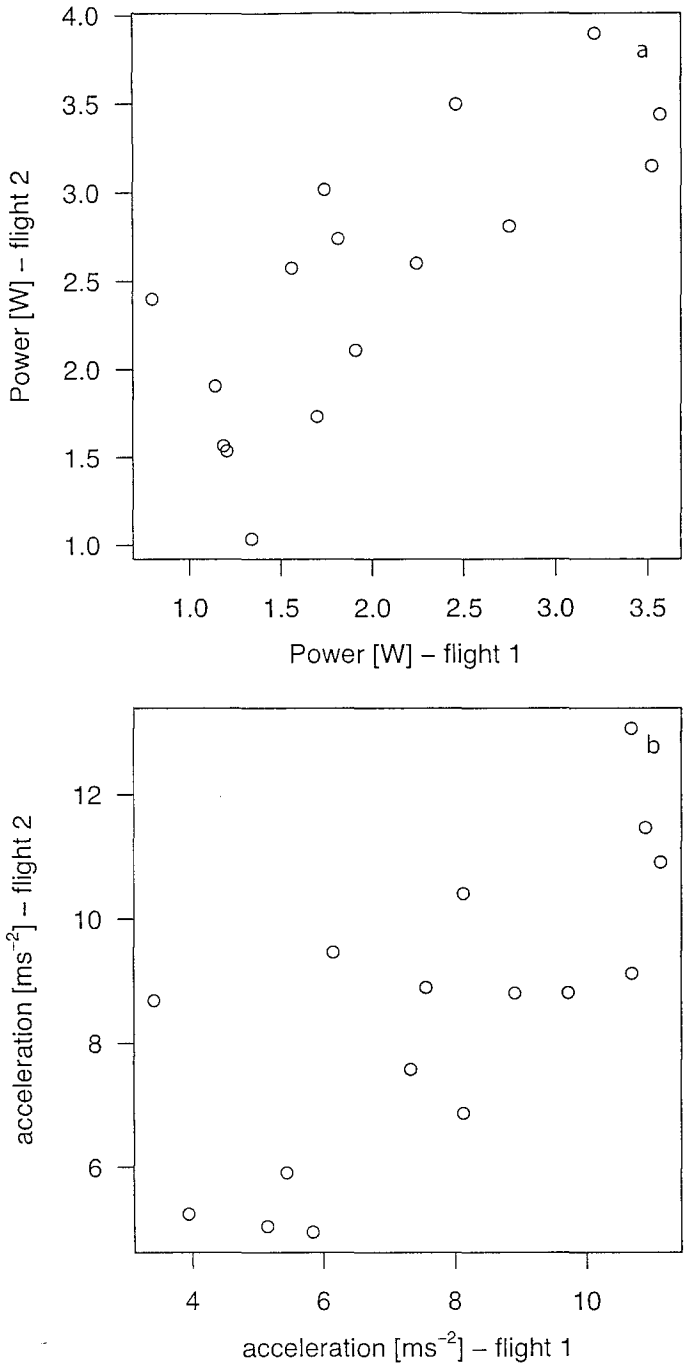


Figure 4.5 Acceleration (a) and power output (b) of Least Auklet flights, 0.17 s after take-off. Plotted are two take-offs of each individual to demonstrate repeatability of these measures.

Table 4.1 Comparison of repeatability of take-off parameters of 202 Least Auklet (*Aethia pusilla*) take-offs from Buldir Island in 2002. Shown are repeatability (r), associated probability (P), repeatability after correcting for differences in slope (sin (Θ) – see text), average n (n0), and regression between the measure and slope (Θ) with parameter estimates for slope and intercept. Mean acceleration was taken between 0 and 0.2 seconds after take-off. Distance was measured along the trajectory and projected onto the horizontal (the lines marked with x). (following page)

							regression with slope					
parameter	time	horiz.	r	p	n0	CV	reg slope	interc	F	df	p	r^2
time [s]	0.5m		0.409	0.07	1.1043	2.233	-0.22	-0.22	1.9	1 198	0.171	0.009
		x	0.081	0.43	1.1043	3.617	-0.34	-0.43	4.8	1 198	0.029	0.024
velocity [ms^{-1}]	optim.		0.565	0.01	1.1037	0.1579	-1.00	2.30	4.4	1 199	0.036	0.022
		x	0.371	0.11	1.1004	0.1649	-0.55	3.06	1.0	1 194	0.314	0.005
acceleration [ms^{-2}]	max		0.154	0.33	1.1031	0.2903	-10.53	-4.93	22.6	1 200	0.000	0.101
		x	0.136	0.36	1.1031	0.3245	-8.20	-2.20	11.8	1 200	0.001	0.056
	optim.		0.720	0	1.1031	0.3966	-11.24	-8.51	25.0	1 200	0.000	0.111
		x	0.624	0.01	1.1037	0.4010	-13.09	-11.86	41.5	1 199	0.000	0.173
	0s - 0.2s		0.600	0.01	1.1031	0.2751	-8.92	-5.37	36.0	1 200	0.000	0.152
		x	0.534	0.02	1.1031	0.2864	-4.07	0.46	8.4	1 200	0.004	0.040
force [N]	max		0.072	0.44	1.1031	0.2977	-0.89	-0.46	23.7	1 200	0.000	0.106
		x	0.020	0.51	1.1031	0.3300	-0.70	-0.24	12.9	1 200	0.000	0.061
power [W]	max		0.235	0.23	1.1031	0.5780	-7.25	-6.75	21.0	1 200	0.000	0.095
		x	0.380	0.09	1.1031	0.6189	-6.31	-5.84	17.7	1 200	0.000	0.081
	optim.		0.750	0	1.1031	0.4764	-3.30	-2.75	21.8	1 200	0.000	0.098
		x	0.671	0	1.1037	0.4877	-2.61	-2.10	17.5	1 199	0.000	0.081
sin (slope)			0.179	0.3	1.1031	-0.0620						

Given the same wing length, a heavier bird would be expected to be a weaker flyer, accelerating more slowly and reaching a lower velocity in a set period of time. In a two-factor multiple regression (without interactions), I tested velocity along the horizontal, acceleration, and power, each at their respective optimal times, against mass and wing length. The models for velocity and acceleration were not significant ($F = 0.245$ df = 2,229, $P = 0.78$ and $F = 0.30$, df = 2, 234, $P = 0.74$, respectively). The model power ~ mass + wing was significant, ($F = 3.06$, df = 2, 232, $P = 0.049$) however with mass being the significant independent variable (Table 4.2).

Table 4.2 Multiple regression model of Least Auklets mechanical power output (∂Energy/∂t) at t = 0.17 seconds after take-off.

	Estimate	SE	t	P
(Intercept)	0.987	2.939	0.34	0.737
mass	0.034	0.014	2.46	0.015
wing length	-0.017	0.031	-0.55	0.584

While there was no effect of mass on velocity or acceleration within Least Auklets, Crested Auklets (which have over three times the mass of Least Auklets) showed significantly lower acceleration values (projected onto the horizontal, averaged over the first 0.2 seconds after take-off) than Least Auklets (Table 4.3). The trajectory of Crested Auklets was also significantly steeper than that of Least Auklets. In most other measures

of velocity and acceleration, Least Auklets were slightly faster than Crested Auklets, although not necessarily significantly so (Table 4.3). Maximum acceleration recorded was 24.25 m s^{-2} for Least Auklets, and 20.81 m s^{-2} for Crested Auklets. Since acceleration and velocities were similar between the two species, but Crested Auklets having a mass over three times that of Least Auklets, the resulting values for power and force were significantly greater in Crested Auklets.

Table 4.3 Comparison of take-off parameters between Least Auklets and Crested Auklets from Buldir Island in the years 2001 and 2002. Distance was measured along the trajectory as well as along the horizontal (marked x). (following page)

			Least Auklet					Crested Auklet							
parameter	time	horiz.	mean	se	range		n	mean	se	range		n	t	df	p
time [s]	0.5m		0.103	0.011	-0.20	0.30	271	0.204	0.016	-0.20	0.30	40	-3.49	309	0.001
		x	0.059	0.011	-0.20	0.28	271	0.158	0.019	-0.20	0.23	40	-3.25	309	0.001
velocity [ms^{-1}]	optim.		3.738	0.040	1.75	6.55	272	3.705	0.068	2.72	4.57	40	0.30	310	0.764
		x	3.763	0.044	1.43	6.26	260	3.537	0.083	1.82	4.76	40	1.94	298	0.053
acceleration [ms^{-2}]	max		10.247	0.193	3.81	24.25	274	9.891	0.535	5.25	20.81	40	0.65	312	0.513
		x	9.590	0.204	3.39	23.64	274	8.982	0.629	3.81	23.86	40	1.04	312	0.300
	optim.		7.452	0.188	-4.56	19.64	274	7.545	0.370	3.35	11.86	40	-0.18	312	0.855
		x	6.528	0.174	0.08	16.32	272	6.135	0.335	1.99	9.46	40	0.83	310	0.405
	0s - 0.2s		7.481	0.139	1.25	18.04	274	7.303	0.293	3.80	11.27	40	0.47	312	0.641
		x	6.288	0.125	-0.21	15.92	274	5.500	0.208	3.10	8.24	40	2.34	312	0.020
force [N]	max		0.826	0.016	0.28	1.85	273	2.597	0.165	1.47	4.97	26	-24.79	297	0.000
		x	0.773	0.017	0.26	1.80	273	2.332	0.202	1.22	5.70	26	-19.16	297	0.000
power [W]	max		3.316	0.123	0.72	13.47	273	11.173	1.473	4.39	33.65	26	-13.12	297	0.000
		x	2.840	0.115	0.00	13.22	274	6.412	1.225	0.00	34.01	40	-6.46	312	0.000
	optim.		1.966	0.063	-0.78	7.24	273	6.716	0.385	3.13	10.54	26	-20.21	297	0.000
		x	1.587	0.054	0.03	6.06	271	4.627	0.292	1.71	7.57	26	-15.43	295	0.000
sin (slope)			-0.717	0.006	-1.73	-1.04	274	-0.763	0.015	-1.75	-1.30	40	5.40	312	0.000

Discussion

In this study I evaluated a method for measuring take-off acceleration and velocity under field conditions using readily available consumer-grade digital video equipment. Interpolation of deinterlaced video-frames effectively doubled the frequency to 59.94 frames s^{-1} , making it feasible to make precise estimates of acceleration. Repeated measurements of the same individual on different days demonstrated high repeatability for power, acceleration, and, to a lesser degree, velocity measurements. Variation in the horizontal component of velocity and acceleration, at the respective time of maximum repeatability, was significantly greater amongst individuals than within repeated take-offs of the same individual. This suggests that the take-off parameters power, acceleration, and velocity could be suitable indicators of an auklet's ability to evade predation and its overall flying performance. Time taken to traverse a set distance, as used in recent studies (e.g., Kullberg *et al.* 2002b), still had a significant repeatability but appeared less suitable.

The measures with the highest repeatability found in this study were power and acceleration, each projected onto the horizontal, 0.17 seconds after take-off (75 % and 72 % respectively, Table 4.1). By comparison, external morphometrics of Crested Auklets were measured with repeatabilities between 88 % and 97 % within, and between 22 % and 91 % among observers (Jones *et al.* 2000), the scoring of their crests in the field had a repeatability of 70 % (Jones, and Hunter 1999). Repeated hematocrit readings of Barn

Swallows (*Hirundo rustica*) had a repeatability of 91 % (Saino *et al.* 1997), as examples of behavioural repeatability, different aspects of the mate choice behaviour of female guppies (*Poecilia reticulata*) had a repeatability between 5 % and 35 % (Brooks 1996); repeatability of courtship behaviour in the housefly (*Musca domestica*) ranged from 30 % to 50 % (Aragaki, and Meffert 1998); and the nesting behaviour in a turtle had a repeatability of 20 % (Janzen, and Morjan 2001). I am not aware of a study of the repeatability of flight performance in birds. There are, however, a number of studies reporting repeatability values of performance in fish, amphibians, and reptiles (Kolok 1999). The repeatability of maximum burst speed of Malibu tadpoles, for example, was 65 % (Watkins 1997).

Repeatability of time-dependent measures varied considerably over the course of a take-off, probably due to both inherent features of a take-off as well as measurement errors towards the edge of the video frame. Due to this variation, it seems important to determine the optimal time to sample velocity, acceleration, or power empirically. Auklets that made a turn rather than flying straight, are the likely cause of the slight dip towards the end of the velocity profile, rather than the bird actually slowing down. Evidently, auklets can reach much higher speeds than the 4 - 6 m s^{-1} observed in this experiment: When auklets fly straight down the 45° talus slope even hunting Peregrine Falcons are not always able to catch up with them. Similarly, Marbled Murrelets (*Brachyramphus marmoratus*) fly at a mean velocity of 33 m s^{-1} when flying out to sea, as measured by radar (Burger 1997). While possible, it seems unlikely that auklets would use the "turning gambit" (Howland 1974) right after take-off, i.e., deliberately slowing

down so as to make a tighter turn. If this ever happens, then it probably only occurs immediately before a turn is initiated.

Much attention has been given to peak acceleration. In the current scenario, the final velocity reached might be more important than an initial burst of acceleration, because auklets are commonly caught after a longer chase rather than within a second of take-off (MR, unpubl. observ.). Contrary to expectations, repeatability of maximum acceleration was poor. Repeatability of acceleration (72 %) and velocity (56.5 %) were high at empirically determined time intervals after take-off and should be used in studies interested in using take-offs or fast-starts as an indicator of performance or some other intrinsic quality.

The failure to find a significant relationship between mass and take-off performance could be based on the comparatively low variability of mass. So far, mainly studies looking at migratory fuel loads have been able to detect such an effect (Lind *et al.* 1999; Kullberg *et al.* 2000; Burns, and Ydenberg 2002), but see Kullberg et al. (2002a; 2002b). This lack of a significant relationship between mass and take-off performance does not support the programmed mass loss hypothesis; however, it should not be viewed as evidence against this hypothesis either. It could also be caused by weaker birds adjusting their mass in order to maintain flying performance, thereby trading off the risk of starvation against the risk of predation. A more rigorous test would involve experimental manipulation of the bird's condition, for example through supplementary feeding or handicapping. Questions remain as to whether the observed drop in adult body mass after hatching is due to food stress or an adaptive strategy to save energy by making foraging

flights more energy efficient. While there is evidence supporting a programmed mass loss (e.g. Croll *et al.* 1991; Jones 1994), even penguins show the same pattern (Edge 1996; Renner 1998) and it seems unlikely that the reduced fuel load would significantly reduce hydrodynamic drag.

As expected for their larger size, Crested Auklets had a significantly greater force and power output than Least Auklet (Table 4.3), sufficiently larger so that there were no significant differences in maximum acceleration. Velocity and time to clear the first 0.5 m indicate, however, that Least Auklets were able to take off considerably faster than Crested Auklets. By chasing Crested Auklets rather than Least Auklets, Glaucous-winged Gulls may therefore not only obtain a larger meal, but also one that is easier to catch.

There are few published reports on acceleration measurements in birds. Figure 4.6 compares Crested and Least Auklet data with acceleration and mass data from several passerine and swift species (data from Warrick 1998). After adjusting for differences in air density, both species fit remarkably close to the power function derived from data presented in Warrick (1998) even when extrapolated to Crested Auklets, which are well beyond the range covered by the previous data. The best fitting power function had the form acceleration = $12 * \log(\text{mass})^{-1.1}$.

The present study demonstrates the feasibility of measuring take-off performance in the field. This should open up a promising research approach with potential applications not only in functional biology, but also in ecology and behaviour.

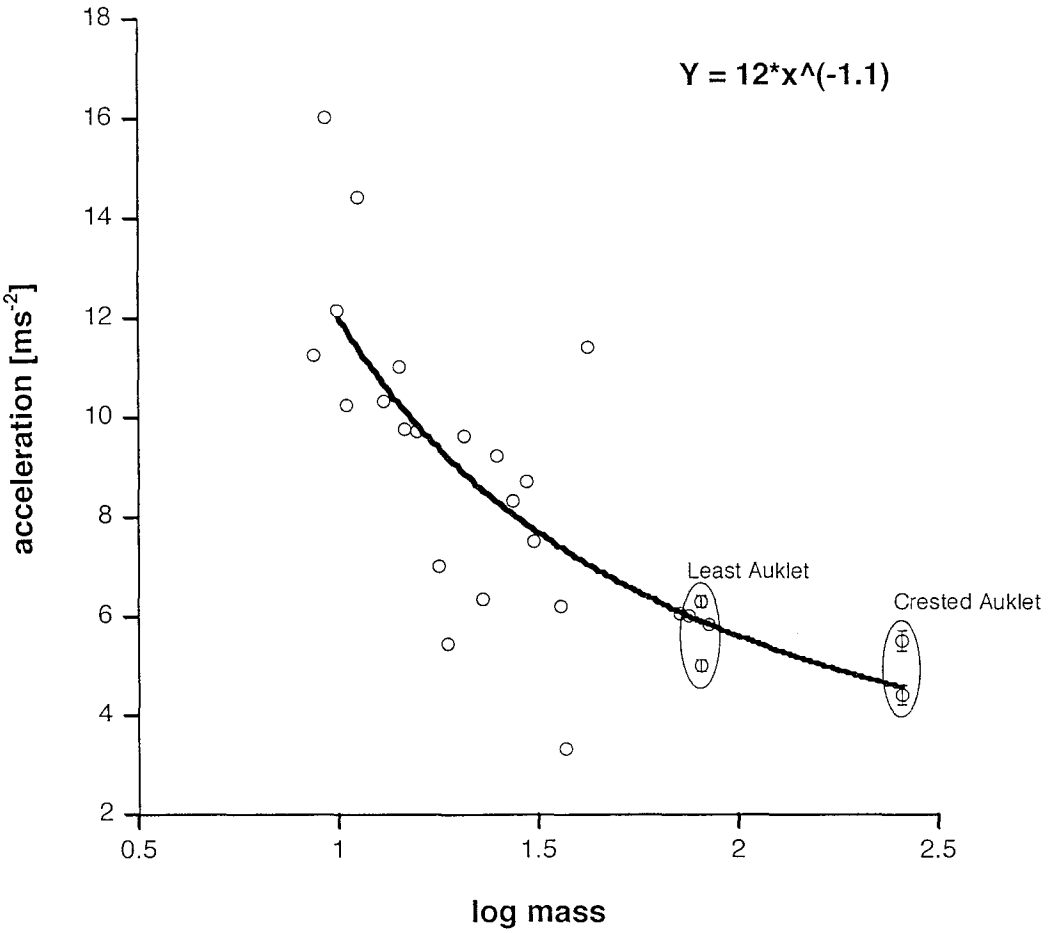


Figure 4.6 Relationship between mean adjusted acceleration and log (mass) of 24 species of North American passerines and swifts (redrawn from Warrick 1998). Least and Crested Auklet are added with an approximate correction for differences in air density (lower values). The power-function was fitted before adding the two auklet species (r^2 = 0.75).

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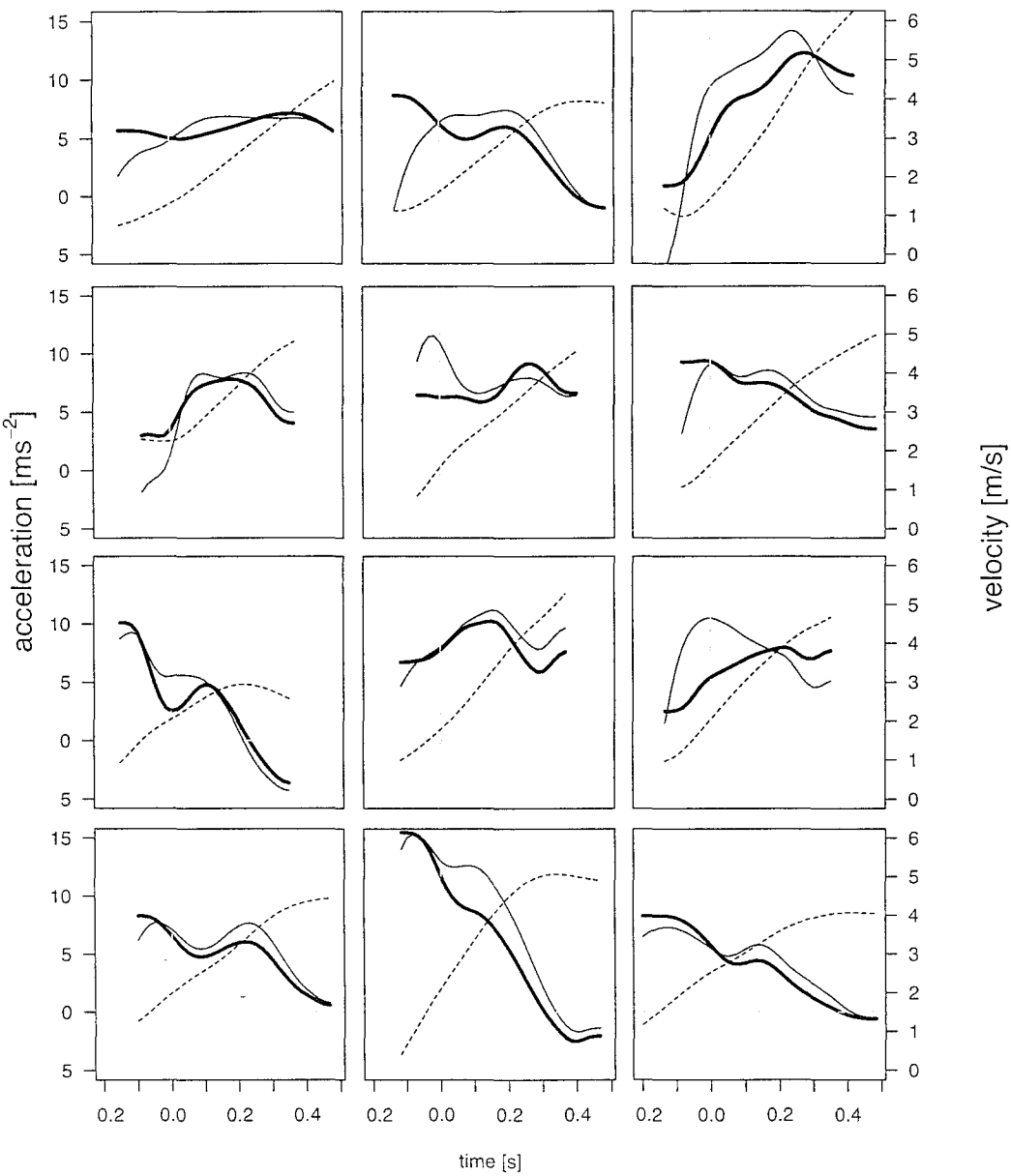
Appendix

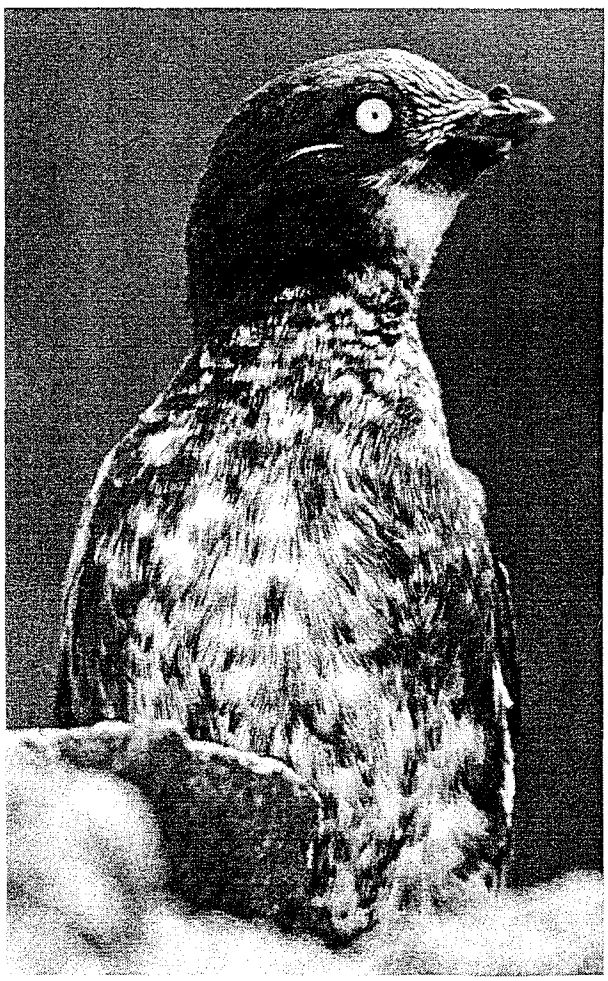
Twelve randomly selected velocity and acceleration profiles. Velocity (dashed) is calculated along the trajectory. Acceleration is shown along the horizontal axis (bold), and along the trajectory (thin).



Chapter 5.

Ornaments in relation to measures of performance and physical fitness in Least Auklets (*Aethia pusilla*)

Martin Renner and Ian L. Jones



Abstract

Conspicuous, variable, but apparently cheap ornaments are a paradox in evolutionary biology. They are common throughout many taxa, including seabirds. The Least Auklet (*Aethia pusilla*), a gregarious, socially monogamous seabird, was used to model expression of two facial ornaments (auricular plume and bill knob) in dependence of parameters linked to fitness (size, mass, hematocrit, leucocrit, take-off acceleration). Both ornaments were significantly positively correlated with size and mass, but not with each other. Bill knob was also correlated with maximum force exerted during take-off. Model selection based on minimizing AIC allowed for interactions with sex, age, year, date, and time of day. Interaction terms turned out to be important, revealing unexpected patterns. Auricular plume length related positively to leucocrit in males but not in females. Body mass (corrected for size) was significantly more strongly related to auricular plume length in subadults than in adults, positive in subadults, no relationship in adults. These results suggest that the mechanisms behind ornament expression are complex and cannot be reduced to "good genes", nor are they a simple indicator of condition. While ornaments are larger in adults than in subadults, but our evidence suggests that they server a more important for subadults, possibly for pre-selecting a mate for the following season.

Introduction

Conspicuous but apparently physiologically cheap ornaments are common in nature. The evolutionary origins of such adornments have been the subject of much debate and remain controversial. If ornaments are used to communicate a meaningful message, then they should have an attached cost (handicap) to ensure that the signal is honest (Grafen 1990a). In birds these low-cost ornaments include visually conspicuous patches and bibs on otherwise unmodified feathers, structurally modified feathers, and, much rarer but also with no great apparent cost, keratinous appendages on the bill. Examples of feather patches are the frontal spot of Pied Flycatchers (*Ficedula hypoleuca*; Lundberg, and Alatalo 1992), facial markings in Red-billed Quelea (*Quelea quelea*; Dale *et al.* 2001), and prominent black patches on the breast ("bibs") of male House Sparrows (*Passer domesticus*; Møller 1987; but also see Griffith *et al.* 1999) and Harris' Sparrows (*Zonotrichia querula*; Rohwer 1975). Structurally modified feathers can be found in numerous birds with crests (over 60 bird species have "crest" in their vernacular English names, after Sibley, and Monroe 1990) and tail ornaments, such as American Barn Swallow (*Hirundo rustica*; Safran, and McGraw 2004). Keratinous appendages on the bill are found for example in the American White Pelican (*Pelecanus erythrorhynchos*), and the Rhinoceros Auklet (*Cerorhinca monocerata*).

Sexual selection for sensory exploitation (Ryan 1990; Ryan *et al.* 1990), may explain the origin of cheap but effectively conspicuous visual traits, but this model does not provide a mechanism to maintain the observed high levels of phenotypic variability within a species. Fisher's runaway process (Fisher 1930; Grafen 1990b; Andersson 1994) predicts that female

preference will drive the expression of ornaments to extremes favoured by mating preferences, but it will be balanced by the high cost of maintenance of the ornaments. If these ornaments are really cheap then what is the explanation for their high variability and how can they convey meaningful signals? If they have hidden costs that ensure honesty, what is the source of these costs? Apparently cheap but highly variable ornaments remain an enigma. Possible solutions to this paradox include weak sexual selection, where other factors are also important in determining the outcome of mate choice in addition to a preference for ornaments (Barlow 1998), or natural selection for optical signals to facilitate individual recognition. The latter case would predict a lack of correlation between multiple ornaments and a frequency distribution approaching uniform or multimodal density rather than a normal distribution (Dale *et al.* 2001).

Condition indices are popular and continue to be recommended (Jakob *et al.* 1996) as proxies for an individual's physical fitness (which in turn should be related to evolutionary fitness). The underlying assumption is that a relatively heavy individual has had the ability to build up greater lipid reserves or muscle mass and is generally more capable of breeding successfully or surviving. If this is true and physical fitness is reflected in the size of an individual's ornaments, one expects a positive relationship between the condition index and ornamentation. This relationship has been found in a number of studies (Andersson 1994), but there are also highly ornamental species that do not display this relationship (e.g. Ruff *Philomachus pugnax* Dale *et al.* 2001; Red-tailed Tropicbird *Phaethon rubricauda* Veit, and Jones 2003) – and publication bias has probably favoured studies where relationships were found. Unfortunately, condition indices are plagued by both statistical flaws and biological problems (García-Berthou 2001; Hayes, and Shonkwiler 2001). The basic assumption in many studies that use condition indices is that relative mass is related to fitness. This is surely the case when food

is limiting and some individuals are on the brink of starvation, but little is known about the shape of the condition-fitness curve when food is at high or even average levels of abundance. Especially during periods of high flight activity, such as during chick provisioning (Jones 1994) or in the presence of predators (Gosler *et al.* 1995; Carrascal, and Polo 1999; Kullberg *et al.* 2000; Krams 2002), a lower mass can be advantageous. The optimal mass within the trade-off between avoiding starvation and avoiding predation would be expected to vary individually depending, for example, on an individual's foraging experience.

Least Auklets (*Aethia pusilla*), the smallest member of the family Alcidae, are highly gregarious, sexually monomorphic, monogamous, diurnal seabirds (Jones 1993). Adults have a small horny knob on the upper mandible at the base of the culmen, white auricular plumes, many small white whisker-like plumes on the forehead, and bill colour varying from black to red with a white tip. None of the Least Auklet's ornaments are as extravagant as those in Crested or Whiskered Auklets (*Aethia pygmaea*), but each varies strikingly among individuals and two (bill colour and auricular plume) were shown to be favoured by mating preferences. The benefit to choosers of mating with ornamented individuals is, however, unresolved (Jones, and Montgomerie 1992). A very weak correlation between an ornament index and a condition index was detected only in one out of three years. In addition to the ornamentation described above, Least Auklets also display a highly variable amount of mottling on the underside (Chapter 6). Because the degree of mottling is correlated with social status (Jones 1990), we also included plumage mottling along with ornaments in this analysis. Why auklets should evolve multiple ornaments (see Møller, and Pomiankowski 1993) has not been addressed. Because auklets moult their body feathers only twice a year (Bédard, and Sealy 1984), and the plumage does not change noticeably at times other than moulting, this information conveyed by plumage mottling will be

useful either only shortly after moult or will have to convey a rather static message over the breeding season.

While it would be best to quantify individual fitness directly (e.g., by observing the number of descendents in the third generation) it is usually more practical to measure a proxy. In this study we measured size, mass, hematocrit, and take-off velocity as indicators of physical fitness, and compared these with measurements of ornaments (knob size, auricular plume length) in Least Auklets on Buldir Island, where avian predation of auklets is common (Chapter 6). Measuring take-off/fast-start performance has become popular, especially in fish and birds (e.g. Webb 1978; Huey, and Hertz 1984; Harper, and Blake 1990; Tobalske, and Dial 2000; Burns, and Ydenberg 2002; Krams 2002; Kullberg *et al.* 2002). Most studies so far have concentrated on the relationship and trade-off between mass and take-off speed. The only study using take-off or fast-start performance as an indicator of fitness examined the effect of pollution on swimming performance of yellow perch (*Perca flavescens;* (Rajotte, and Couture 2002). In Least Auklets, take-off acceleration at 0.17 s after taking flight is a repeatable (72 %) measure of flight performance (Chapter 4). Because rapid take-off is directly related to the bird's likelihood to escape predation, we assume it would serve as a useful indicator of physical fitness. Hematocrit is an easy-to-measure indicator of health (Wanless *et al.* 1997), but can also be elevated in situations of increased stress (Saino *et al.* 1997). Leucocrit is the relative amount of white blood cells. A raised leucocrit could indicate an infection, but also a higher capability to fight infection.

In order to test whether Least Auklet ornaments indicate anything about individual quality, we explored whether Least Auklet ornamentation is a function of mass and size, hematocrit, leucocrit, and take-off performance, while differentiating between the sexes and between adult and non-breeding subadults.

Methods

Least Auklets were caught with noose carpets during their morning activity period on a 100 m^2 study plot high on Main Talus, Buldir Island, Aleutian Islands, Alaska (52° 21'N 175° 56'E) during May-August in 2000, 2001, and 2002. We believe noose carpets select breeding and non-breeding auklets randomly from the local population. Each captured auklet was given an individually numbered stainless steel leg band. Adult birds (for identification criteria of adults and subadults see Bédard, and Sealy 1984) were also given a unique combination of three plastic colour bands. We eliminated five birds from this analysis that we could not age reliably. Upon capture, each bird's mass was measured to the nearest 0.1 g on an electronic balance, and the following linear measurements were taken by MR to the nearest 0.1 mm using dial-callipers: bill depth (twice: 1. from the proximal base of the culmen to the angle of the gonys, and 2. from the tip of the bill knob to the angle of the gonys; knob height was calculated as the difference of these two measures), culmen length, tarsus length (from the mid-point of the tibiotarsal joint to the blunt end of the tarsometatarsal joint on the underside of the foot), and auricular plume length (from the exposed distal end of the plumes just below the eye to the end of the longest plume). Head and bill and maximum wing length (Svensson 1992) were measured with a zero-stop ruler to the nearest 1 mm. For sexing and hematocrit a blood sample, was collected from the brachial vein. We filled a heparinised microcapillary tube (75 μl) for hematocrit determination and preserved up to 250 μl in ethanol for sexing. Each bird's sex was determined using the genetic technique described by Fridolfsson and Ellegren (1999). Plumage mottling was digitally quantified from standardized photographs taken in hand (see Chapter 6).

Hematocrit

Hematocrit tubes were sealed at one end with a crit-o-seal plug, taken back to our base camp and spun usually on the same evening, but always within 72 hours, at 8000 rpm for 5 minutes in a READACRIT™ centrifuge. After centrifugation, MR measured the levels of plasma, leucocytes, and erythrocytes from the top of the tube to the nearest 0.1 mm with dial callipers. To measure evaporation rate, we took six full hematocrit tubes and measured the plasma level nine times over 140 hours (see Appendix). We fit a curve of the form $evaptop(t) = at^b + c$ to the pooled data. After adding the predicted *evatop (t)* to the measured plasma level, we calculated hematocrit and leucocrit as the respective proportion of the blood volume. We did not collect repeated blood samples from a bird over the year to avoid undue stress to individual birds. Although we do not have the data to estimate repeatability of hematocrit in this study, we have no reason to believe that Least Auklet hematocrit fluctuated more than in barn swallows (*Hirundo rustica*), where it was found to be highly repeatable (Saino *et al.* 1997).

Take-off acceleration

As a measure of performance we measured take-off speed and acceleration, which were obtained from single-frame analysis of the position of each bird's eye after release on 60 frame/second de-interlaced digital video files. Time-location data was scaled, corrected for perspective errors, and smoothed with a MSE quintic spline (Craven, and Wahba 1979; Woltring 1985; Walker 1998). The first and second derivative of the spline function with respect to time provided estimates of instantaneous speed and acceleration, respectively (see Chapter 4 for details). Acceleration at t = 0.17 s after the bird lost touch with the take-off pad was the most

repeatable measure of flight performance (r = 72 %) and was used as an indicator of physical fitness.

Statistical analysis

Our dataset is complex in that it involves multiple predictor (indicators of physical fitness) and multiple response variables (ornaments). Furthermore, we expect different responses between age groups and possibly sexes. Any of these factors, or combinations of them, might be appropriate as covariates. For mass, take-off acceleration, and body measurements, we often had multiple records for an individual bird within a year; for some birds we had several years of data. To avoid problems due to lack of independence of multiple records from the same individual, we averaged all values within an individual within a year. For individuals with multiple years of data, we used the year with the most observations and disregarded the other years. The original 485 records were thereby reduced to 353 records. To characterize differences in ornament expression between age classes and sexes, we used a two-way ANOVA.

We pose three questions: 1. Is there evidence for selection for individual recognition in the form of departure from a normal distribution of ornament expression? 2. Is an index of combined ornament expression related to a combined index of physical fitness? 3. Are specific ornaments related to specific indicators of physical fitness? The latter question is problematic from a statistical point of view since it incorporates a multitude of possible tests. This increases the likelihood of type I error if no adjustments to standard tests are made, and adjustments greatly reduce statistical power, especially if a large number of tests are undertaken. There is no one good solution, we report raw P-values but point out that some adjustment is prudent.

To test the hypothesis of individual recognition (question 1) we tested for correlations between ornaments and plumage. We also inspected scatterplots and histograms for evidence of dispersion toward the extremes rather than clustering near the mean.

To address question two, we first combined auricular length and bill knob height by extracting the first major axis of a principal component analysis (PCA) of these two variables. Prior to calculating any PCA, we standardized all variables to give them equal variances and thereby equal weight. As with the ornaments we used PCA to build a combined indicator of physical fitness from mass, take-off acceleration, hematocrit, and leucocrit. To test for a relationship between the ornament and the physical fitness index, we first used a simple linear regression model. We expect mass in particular to undergo seasonal changes (Jones 1994). There might also be differences between years, age classes, and the sexes. To increase the power of our test, we built a second linear model in which we added age (adult vs. subadult), sex, year, and season (Julian date) as covariates. To avoid including unnecessary covariates, we used a stepwise model building approach (Venables, and Ripley 2002). We started with a full model PCA (ornaments) = β PCA (physical fitness) + β age + β sex + β year + β season + ε with one-way interactions. At each step we removed or added the non-marginal term, that would minimise Akaike's An Information Criterion (AIC). We allowed up to two-way interactions and restricted the simplest model to include at least the ornament index. Our full dataset contained many of empty cells, e.g., when no sexing data were available. For the stepwise model selection, we could use only complete records. To maximise statistical power, we fitted the final model structure to the full data set.

To answer question three, whether specific ornaments and plumage mottling are indicative of specific aspects of physical fitness, we built a regression model for each combination,

selecting covariates by minimizing AIC, as described above. In the case of mass we added one additional covariate "size" in form of the first major axis of a PCA of bill depth, head and bill, tarsus, and wing length (loadings: bill depth: 0.524, head+bill: 0.564, tarsus: 0.470, wing length: 0.432). We only used size here as a covariate for mass to take the effect of size on mass into account. Each of these measures were highly significantly correlated with body mass ($P < 0.0001$) indicating that they were indicative of size. For acceleration we added the sine of the take-off trajectory (Chapter 4). By using size as a covariate we avoided the difficulties inherent to condition indices (García-Berthou 2001; Hayes, and Shonkwiler 2001). For each model, we tested the significance of a non-marginal term containing the to be tested physical fitness indicator by comparing the full model with a model reduced by that term ("dropterm" see, Venables, and Ripley 2002). Plotting the effects of significant models revealed the direction of any relationships discovered. Statistical computations were performed in R 2.0.1 (R Development Core Team 2004) on an Apple Macintosh G4.

Results

Auricular plumes were significantly longer in males than in females and shorter in subadults than in adults (Figure 5.1). Size of the bill knob did not differ significantly between ages but males had significantly longer bill knobs than females. Plumage mottling was darker in subadults than in adults but we did not find a significant difference between sexes. An interaction term was not significant in any of the three models ($P > 0.5$), and was therefore omitted.

The ornaments bill knob and auricular plume length were not significantly correlated (Table 5.1). There were highly significant (but weak) correlations, however, between each

ornament and the amount of plumage mottling. Bill knob height was positively and auricular plume length was negatively related to plumage mottling. Scatterplots of ornaments and plumage did not reveal dispersion of data points towards the extreme values nor a deviation from a normal distribution (Figure 5.2), as would be expected under the individual recognition hypothesis. The PCA combining all ornaments resulted in a first major axis with the loadings: auricular: 0.32, bill knob: 0.688, plumage mottling: 0.652 (46 % of variance).

Table 5.1 Correlations among Least Auklet (*Aethia pusilla,* adult and subadults combined) ornaments and the amount of plumage mottling. Pearson correlation coefficients are presented with their confidence intervals above the diagonal; the corresponding P values (and sample sizes) are below the diagonal. Significant P values are set in bold.

	auricular	bill knob	plumage mottling
auricular		0.10	-0.182
		(-0.006- 0.204)	(-0.310 - -0.048)
bill knob	0.064		0.196
	(341)		(0.062 - 0.324)
plumage mottling	**0.008**	**0.004**	
	(209)	(209)	

Table 5.2 Correlations among indicators of physical fitness in Least Auklets (*Aethia pusilla*). Pearson correlation coefficients are presented with their confidence intervals above the diagonal, the corresponding P values (and sample sizes) are below the diagonal. Significant P values are set in bold.

	mass	acceleration	hematocrit	leucocrit
mass		0.102	-0.172	-0.026
		(-0.042- 0.142)	(-0.321 - -0.016)	(-0.183 - 0.132)
acceleration	0.163		0.129	-0.085
	(188)		(-0.106 - 0.350)	(-0.311 - 0.150)
hematocrit	**0.032**	0.280		-0.234
	(156)	(72)		(-0.08 - -0.377)
leucocrit	0.746	0.478	**0.003**	
	(156)	(72)	(156)	

Among the indicators of quality used here, hematocrit and mass showed the strongest correlation with r = -0.172, P = 0.032 (Table 5.2). Hematocrit and leucocrit showed a negative correlation (r = -0.125, P = 0.055), all other correlations were not statistically significant. The PCA combining all indicators of quality resulted in a first major axis with the loadings: acceleration: -0.021, hematocrit: 0.704, leucocrit: 0.541, mass: -0.46 (32 % of variance).

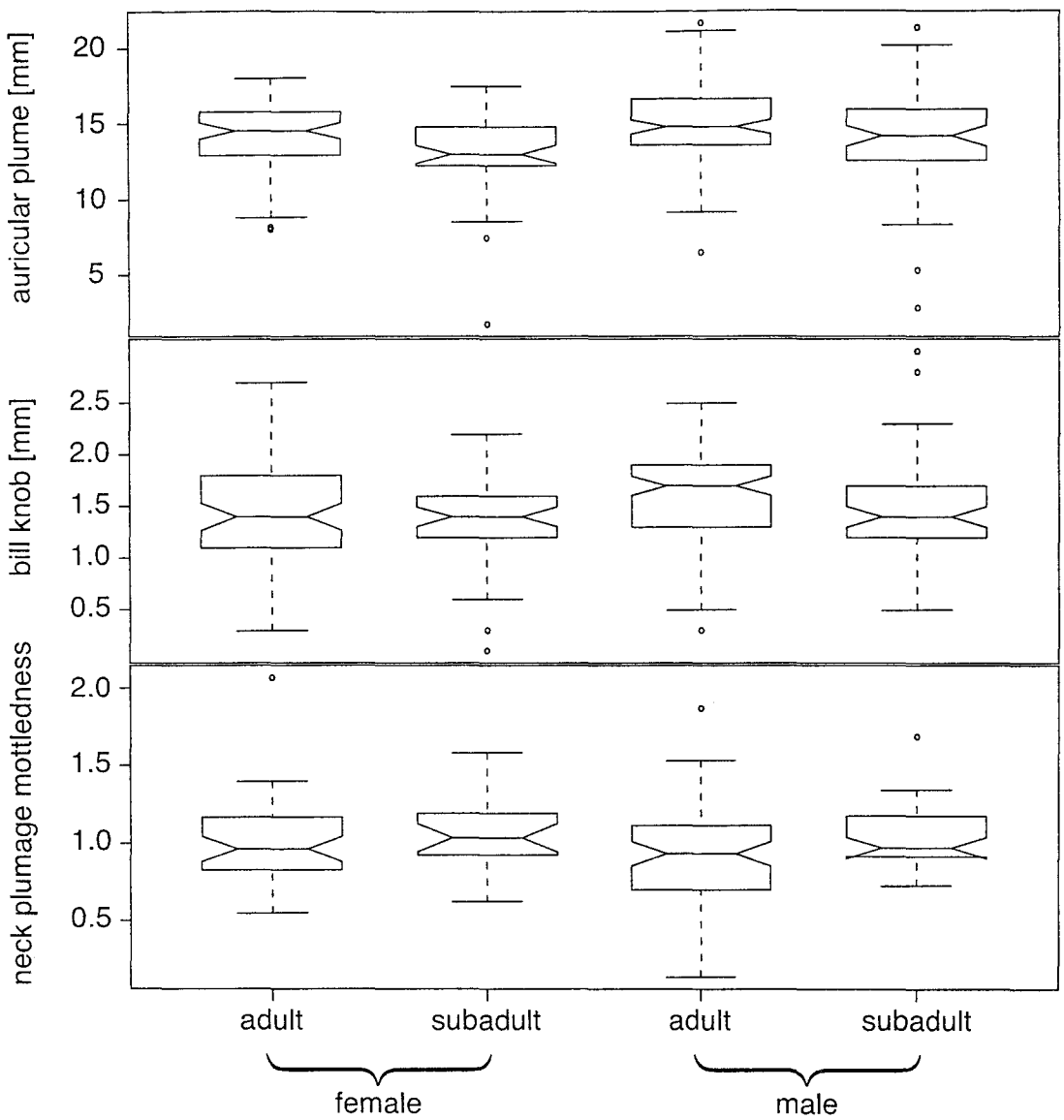


Figure 5.1 Length of the Least Auklet auricular plumes (a), bill knob height (b), and plumage mottledness compared between sexes and ages. Auricular plumes differed significantly between sexes (two-way ANOVA: $F = 6.91$, $df = 1, 278$, $P = 0.001$) and between ages ($F = 10.88$, $df = 1, 278$, $P = 0.009$). Height of the bill knob did not differ significantly between ages ($F=1.54$, $df = 1,278$, $P = 0.215$) but was significantly larger in males than in females ($F = 7.77$, $df = 1,278$, $P = 0.005$). Subadults had a significantly darker plumage on the neck ($F = 5.87$, $df = 1, 169$, $P = 0.016$) but plumage mottledness did not differ significantly by sex ($F = 2.78$, $df = 1, 169$, $P = 0.096$).

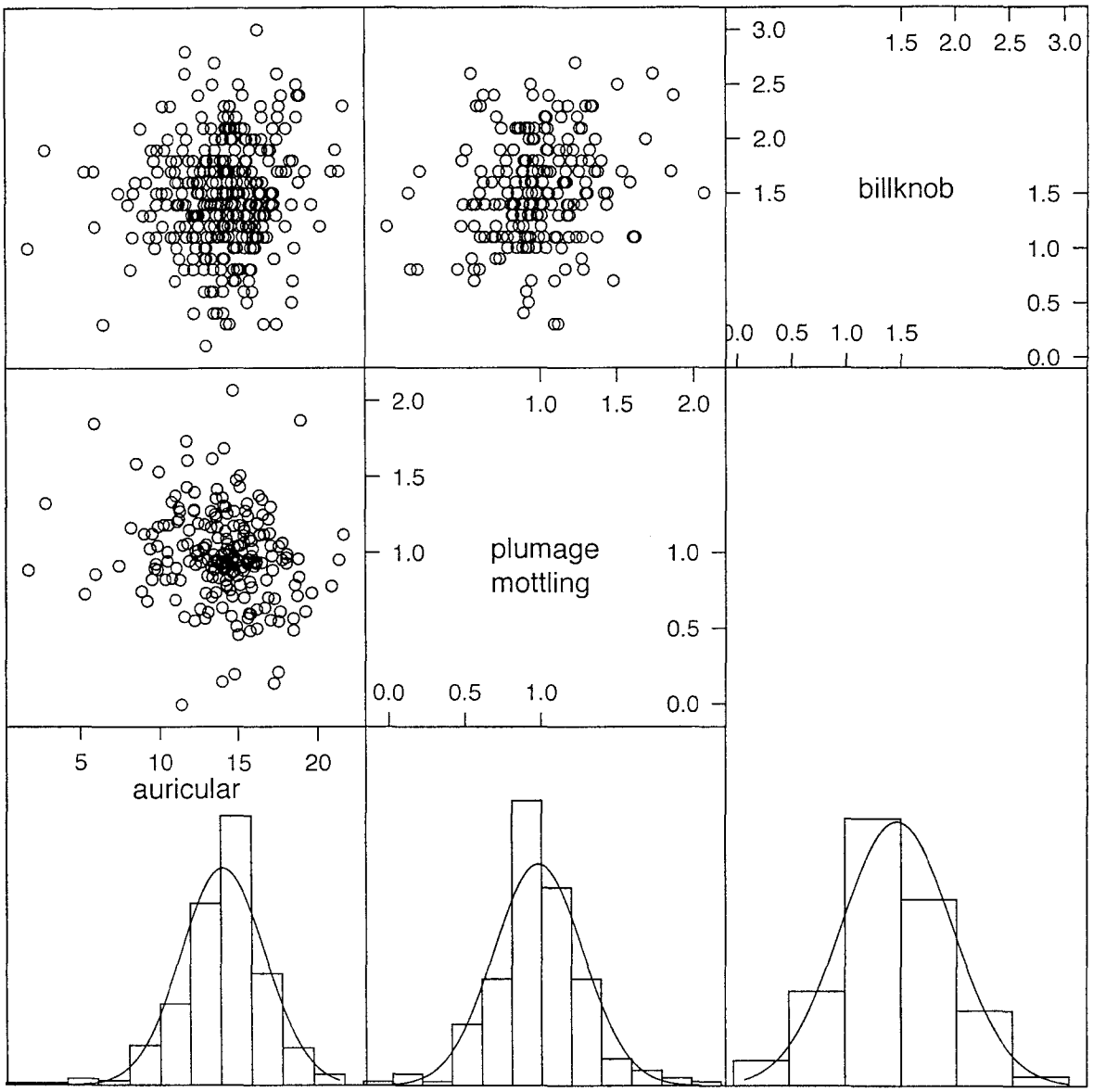


Figure 5.2 Multivariate distribution between ornaments and plumage. The histograms are plotted on a density scale with an overlaid normal distribution with the same mean and standard deviation as the variable under investigation. Scatterplots show the bi-variate pattern between the intersecting variables. No evidence of dispersion or deviation from a normal distribution is apparent, as would be expected under selection for individual recognition.

We found no simple significant relationship between the physical fitness PCA and the ornament PCA ($F = 0.81$, $df = 1,47$, $P = 0.37$). Adding covariates while minimizing the model's AIC did not reveal a significant relationship between the two PCA scores either ($F = 0.05$, $df = 1,45$, $P = 0.83$). The covariates remaining in the model were year ($F = 4.35$, $df = 1,45$, $P = 0.04$) and sex ($F = 4.22$, $df = 1,45$, $P = 0.04$). Body mass did not show marked systematic fluctuations over the time frame considered and Julian date was eliminated in the model-building process.

The results of modelling each ornament against each indicator of physical fitness are summarised in

Table 5.3. Including covariates and interactions revealed at least one significant relationship, with a physical fitness indicator for each ornament. In each of these models, the physical fitness indicator was involved in a significant interaction with age, sex, or date. For each of the ornaments and plumage we found a significant interaction between mass and age (Figure 5.3). In the case of bill knob height and auricular plume length, there was essentially a flat relationship between ornament expression and body mass in adults, but a positive relationship in subadults. The statistically significant interaction means that there is a difference in slope between the two regression lines. In contrast to the two structural ornaments, plumage mottledness showed a negative relationship with mass in adults but not in subadults, i.e. light-plumaged adults were heavier than dark-plumaged adults. Auricular plume length was also related to leucocrit levels, negatively in females and positively in males (Figure 5.4). The relationship between bill knob height and acceleration during take-off varied between years. It was negative in 2001, but positive in 2002 (Figure 5.4).

Table 5.3 Models of Least Auklet ornament expression as a function of indicators of physical fitness.

auricular	interact	F	df	P		r^2	covariates
mass	age	8.81	1, 265	0.003	**	0.11	sex, year, date:size
acceleration	/	2.28	1, 132	0.133		0.09	sex:year, age:year
hematocrit	/	0.62	1, 135	0.433		0.11	sex:age
leucocrit	sex	6.98	1, 135	0.008	**	0.14	age
bill knob							
mass	age	4.43	1, 264	0.036	*	0.2	sex, size, age:date
	date	2.60	1, 264	0.108			
acceleration	year	5.70	1, 132	0.018	*	0.32	sex, date:year
hematocrit	/	3.40	1, 134	0.067	.	0.22	age:date, sex
leucocrit	/	0.35	1, 134	0.550		0.20	age:date, sex
plumage							
mass	age	11.0	1, 154	0.001	**	0.35	year:date, age:date, date:sex,
	size	8.31	1, 154	0.005	**		year:size
	date	2.67	1, 154	0.104			
	year	1.86	1, 154	0.174			
acceleration	/	0.07	1, 99	0.785		0.08	age, year
hematocrit	/	0.41	1, 81	0.520		0.38	age:date, sex:date, age:year
leucocrit	year	0.01	2, 81	0.942		0.38	date:year, sex:year, age:date

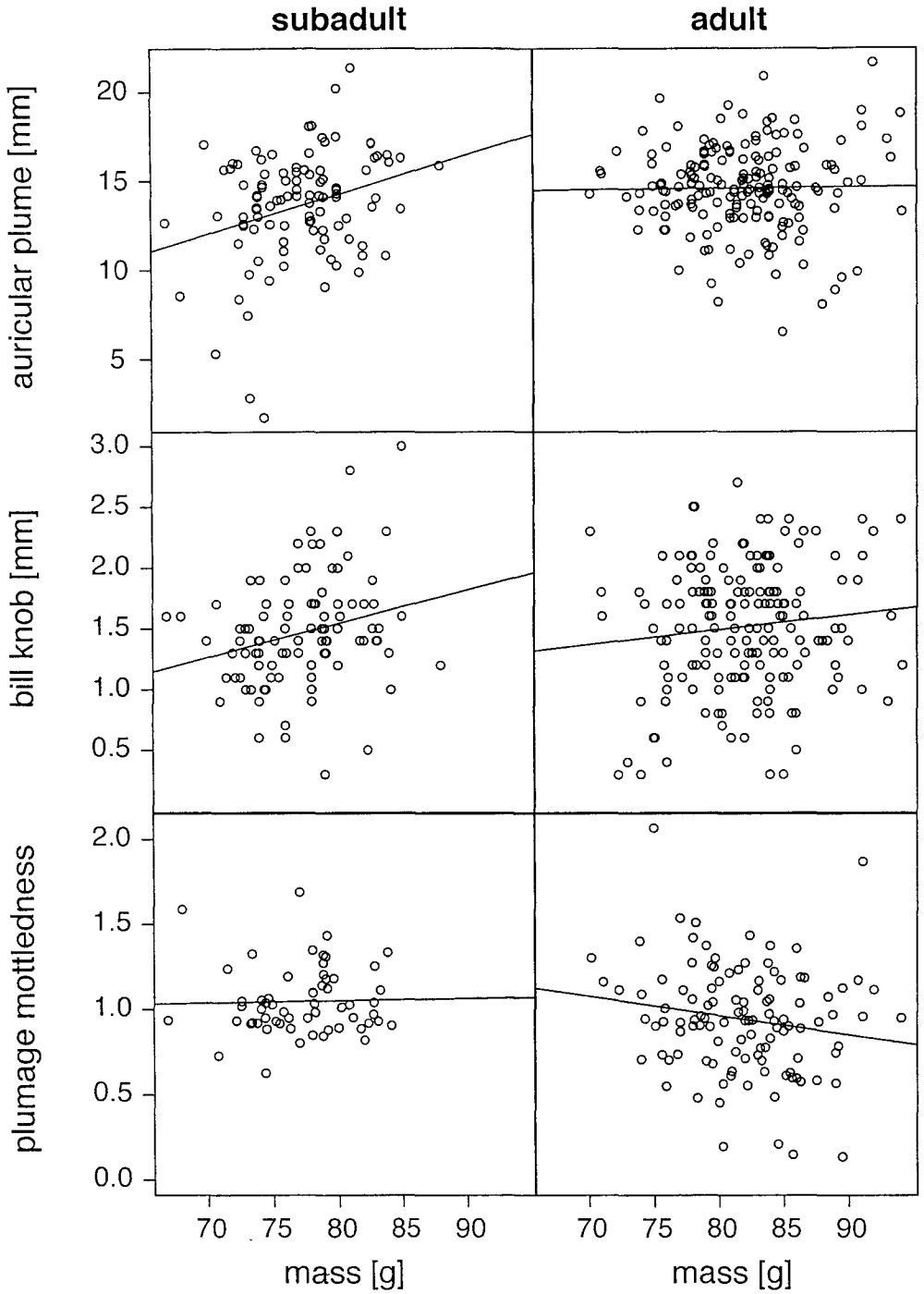


Figure 5.3 Relationships between Least Auklet ornaments (including plumage) and body mass are characterised by statistically significant interactions (once other covariates are considered - see

Table 5.3.

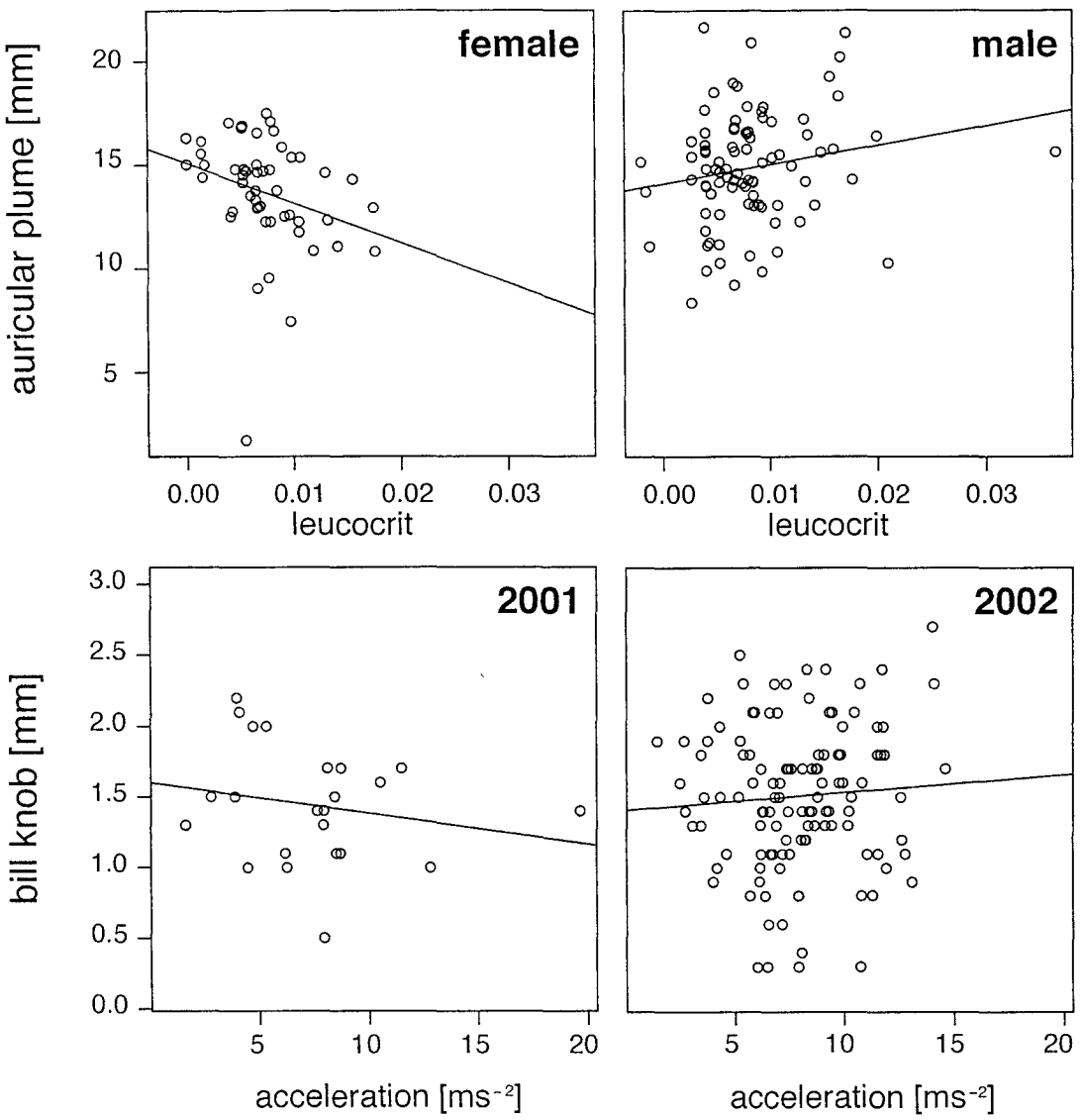


Figure 5.4 Further relationships between Least Auklet ornaments and indicators of physical fitness involving interactions with sex and year.

Discussion

Taken together, our data showed that bill knob height and auricular plume length, the ornaments considered here, as well as plumage mottledness, varied with several measures of physical fitness. These relationships only became apparent after allowing for interactions with covariates such as sex and age class. A simple regression approach of a PCA of ornaments against a PCA of physical fitness indicators failed to reveal a relationship. Not only was the correlation among ornaments and among indicators of physical fitness weak (Table 5.1, Table 5.2), some interaction could also mask the existence of a relationship (Figure 5.4).

The modelling approach revealed some complex but significant relationships that were not detected by a simple regression. Most consistently, auricular plume length, bill knob height, and plumage mottledness were all related to body mass, while taking size into account (using a condition index was thereby avoided). However, in each case this relationship was highly age dependent. For both ornaments, subadults showed a significantly stronger relationship between body mass and ornament size than did adults. That subadults would show stronger correlations might be surprising at first, because subadults do not breed. However, subadults spend considerable amounts of time on land the year before they might breed for the first time and may use this time to find a mate for the following season. At St. Paul Island (57°07'N, 170°16'W; 1030 km ENE of Buldir), over 50 % of adults have to find a new partner to mate with because of divorce or death of their mates (Jones, and Montgomerie 1991). Since subadults have never mated (or only in exceptionally rare cases), all subadults have to find a new mate in the following year - double the rate of adults. Selection pressure might therefore act more strongly on

subadults than on adults. These results could therefore be viewed as evidence that subadults search out mates for the following season during their extensive presence on the talus surface. Being more experienced, adults are expected to be better foragers. In an environment of seasonally abundant food, only the weakest, most inexperienced individuals are expected to be limited by food. A relationship between ornament expression and condition would then be only expected for low quality birds.

These results support the hypothesis that ornaments are indicators of some form of physical fitness. It is doubtful, however, that ornaments should have evolved through sexual selection to indicate mass alone, since the relationship found here is rather weak and a potential mate could have more direct ways to assess mass (e.g., by direct comparison with its own body size). While mass is commonly used as an indicator of quality, this relationship is likely to hold true only in situations of food shortage. These conditions are likely to be met more frequently for poor quality individuals. Our results of bill knob height and auricular plume length in subadults are consistent with this explanation. None of the other indicators of physical fitness were paired with age as an interaction. This suggests that there is a (weak) association between quality and ornamentation, even in individuals with an abundant food supply. In those cases, mass is not a suitable indicator of quality.

Blood parameters were not related to plumage mottledness and only hematocrit was weakly related to bill knob height ($P = 0.06$,

Table 5.3). Leucocrit and take-off acceleration presented strong but puzzling patterns with auricular plume length and bill knob height, respectively. The relationship between leucocrit and auricular plume length was negative in females but positive in males. The slope of the relationship between bill knob height and take-off acceleration differed significantly between the 2001 and 2002 (we did not collect take-off data in 2000). We have no ready explanation for these patterns, but like to stress that a single year study or a study not differentiating between sexes might have reached rather different conclusions.

In contrast to Crested Auklets (*Aethia cristatella*) (Jones *et al.* 2000), male Least Auklets had larger ornaments than females on average (Figure 5.1), which are preferred in mate choice (Jones, and Montgomerie 1992). It is also males that perform active advertising vocal and visual displays (Hunter, and Jones 1999). This evidence suggests that the mating system of Least Auklet is biased towards females being the choosier sex. This is further corroborated by the finding that male, but not female, plumage mottling is related to the chance of divorce (Jones, and Montgomerie 1991). Mutual sexual selection, as found in Crested Auklets (*Aethia cristatella*) (Jones, and Hunter 1993) might still occur but, seems to be less important in Least Auklets.

Least Auklets have the social qualities (gregarious, territorial, complex sociality) that would make it a good candidate for selection for individual recognition (Dale *et al.* 2001). In Crested Auklets, ornaments are highly conserved within individuals over several years (Jones *et al.* 2000), meeting another condition for selection for individual recognition. We only found a weak correlation between the ornaments considered ($P = 0.06$, despite $N = 341$, Table 5.1). Correlation coefficients (significantly different from 0) between Crested Auklet ornaments (Jones *et al.* 2000) fall within the confidence intervals of correlations coefficients found here. We also

found a correlation of each ornament with the degree of plumage mottling. More importantly, however, we did not observe positive evidence for selection for individual recognition in the form of a divergence from a normal distribution, but did find relationships with indices of physical fitness. Both of these findings are in conflict with the individual recognition hypothesis.

The handicap theory would predict that if there is no cost, then an ornament cannot be a reliable and evolutionarily stable signal (Grafen 1990a). Therefore, if an ornament has only a small cost associated with it, this signal might be effective only for low quality individuals. We suggest that auricular plume and bill knob might be such low cost signals. They are ineffective for high quality individuals because the cost is insufficient to ensure honesty. Plumage mottling, however, makes a Least Auklet more visible to predatory Glaucous-winged Gulls *Larus glaucescens* (see Chapter 6). So in the case of plumage mottling, there is a tangible cost associated with the expression of this character.

Multiple ornaments could convey different messages that a potential mate could use for a more complex assessment (Møller, and Pomiankowski 1993). We did find that the two ornaments and plumage mottledness all relate to mass in a similar way. Only auricular plume length was related to leucocrit (albeit in different ways between the sexes) and might therefore convey information about an individual's state of health and immune system. Bill knob was related to take-off acceleration; however, since this relationship differed between years, it is unlikely to be of any use in mate choice. This result leads us to point out that the patterns of ornamentation found in birds appear to be far more complex then suggested by most theoretical models, and that we are still a long way from understanding ornaments comprehensively.

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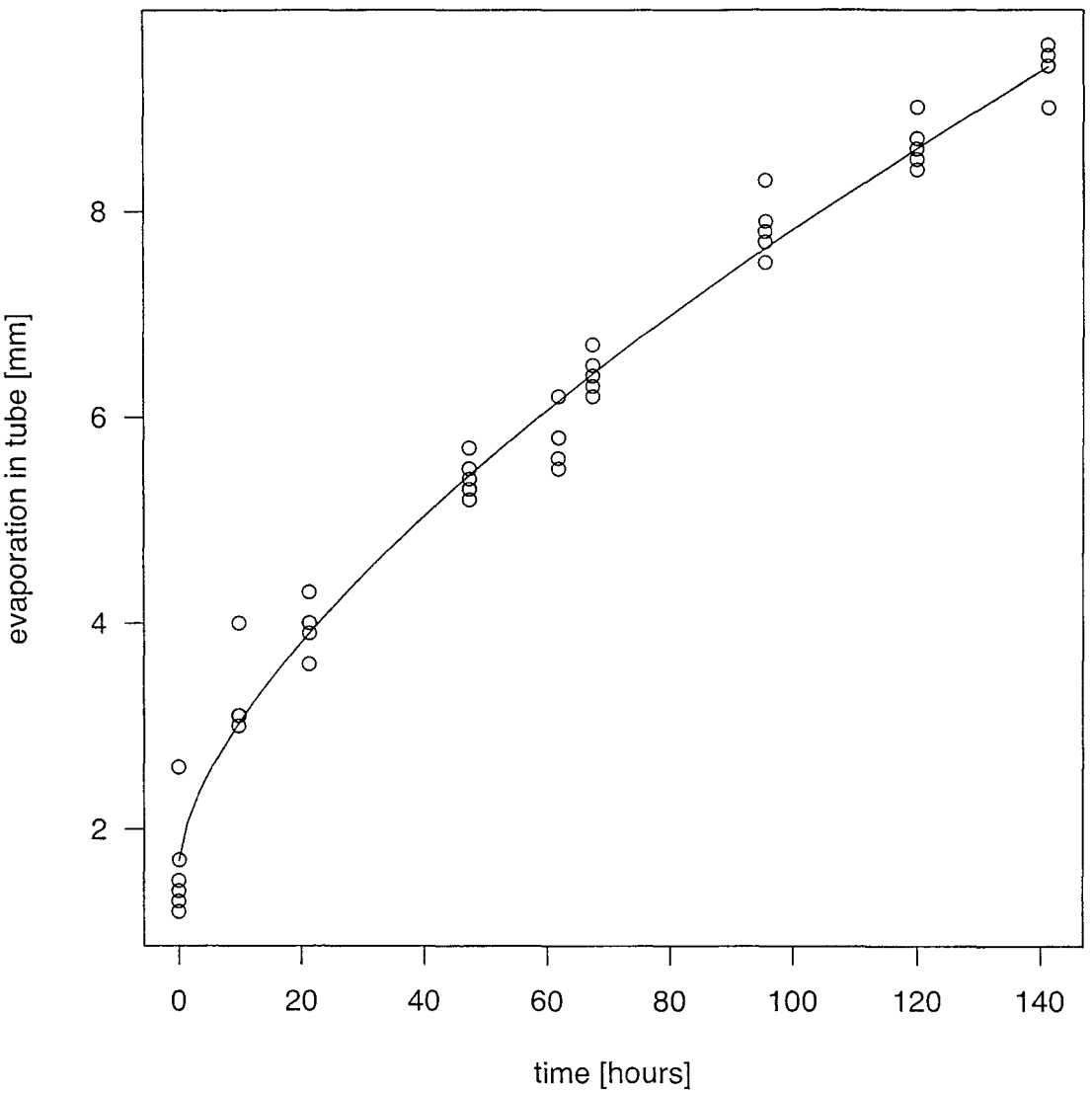
Appendix

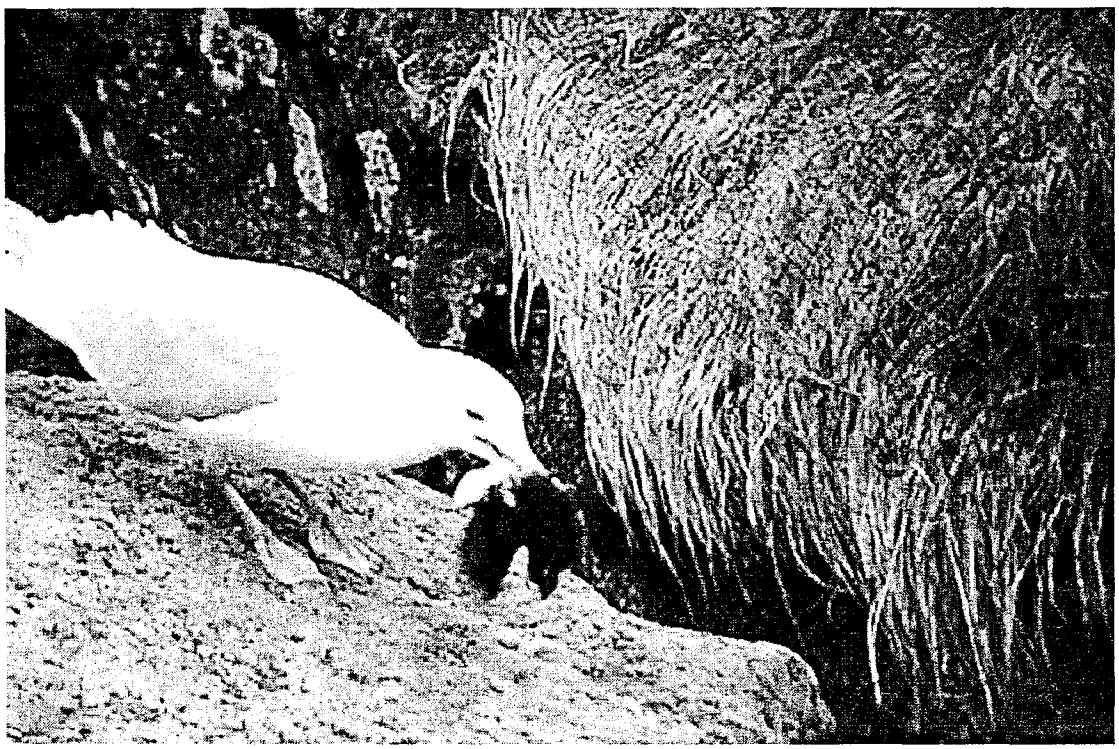


Experiment to correct for evaporation of plasma in hematocrit tube. The plasma level of 6 initially full hematocrit tubes was measured repeatedly over the course of 140 hours. Evaporation was a function of time following: level = 0.290 $mm*h^{-1}$ * $time^{0.661}$ h + 1.693 mm

Chapter 6.

An experimental study of the function of variation in ventral mottling in Least Auklet (*Aethia pusilla*) plumage

Martin Renner and Ian L. Jones



Abstract

Conspicuous variation in plumage colour can be used as an optical signal in social interactions, but might also play a role in predator-prey interactions. A handicap model in predator-prey interactions suggests that conspicuous prey signals low profitability to the predator. This predicts that 1. predators should prefer cryptic prey individuals, 2. that in the absence of predators, conspicuousness is more common, and 3. that conspicuous prey are more capable of escaping. We tested these three predictions for Glaucous-winged Gulls (*Larus glaucescens*) preying on Least Auklets (*Aethia pusilla*), a small seabird of highly variable plumage. In a model experiment, gulls attacked experimentally darkened auklets significantly more often than lightened models ($P = 0.036$). Least Auklets were significantly lighter on an island where gulls were absent, than on an island where gull predation was common ($P < 0.001$). In contrast to the third prediction, however, plumage mottling not related to take-off velocity. Most of these results support the handicap hypothesis for light plumage in Least Auklets, however. Although we did not detect darker birds to be weaker fliers, this effect has been found in other species.

Introduction

Strategies to avoid predation have shaped morphology, external appearance, and behaviour of most animal species. The simplest way to avoid predation is to avoid being detected. Once detection has occurred, however, it is in both participants' best interest if the predator can judge the likelihood of successful capture. That way it can minimize costly fruitless pursuits. The handicap principle (Veblen 1899; Zahavi 1975; Zahavi, and Zahavi 1997) implies that in order to be evolutionarily stable, a signal communicating escape capability needs to involve a cost that outweighs the benefits cheaters would obtain (Grafen 1990; Johnstone, and Grafen 1992). A number of examples for this mechanism have been proposed in which a potential prey engages in energetically expensive behaviour while pursued by a predator (Fitzgibbon, and Fanshaw 1988; Hasson *et al.* 1989; Hasson 1991; Cresswell 1994; Martin, and López 2001). Similarly, warning colours have be viewed as handicaps (Guilford, and Dawkins 1993). Conspicuous colours in birds are often viewed in the context of sexual selection, but at least one case has been made that a bird has evolved aposematic, or warning colouration (Diamond 1992; Dumbacher *et al.* 1992; Mouritsen, and Madsen 1994).

Least Auklets (*Aethia pusilla*), whose underpart pigmentation varies within populations from pure white to nearly black, present a paradox because birds with a large amount of breast pigmentation have a lower dominance status than individuals with little or no pigmentation (Jones 1990). In most species studied, pigmentation is positively related to social dominance or an indicator of quality (e.g., Rohwer 1985; Møller 1987;

Slagsvold, and Lifjeld 1992; Veiga, and Puerta 1996; McGraw *et al.* 2002). The Least Auklet is a socially monogamous, colonial seabird that breeds in crevices on remote islands in the Bering Sea and Sea of Okhotsk. Most Least Auklet breeding colonies are on volcanic islands of basaltic rock where the birds breed on talus slopes with little or no vegetation. This leads to an optical environment of low contrasts dominated by dark grey tones. The winter (basic) plumage of adults and first-year birds shows an all-white underside (Bédard, and Sealy 1984), but during the breeding season a highly variable amount of black spotting is displayed. Extremes in the amount of this mottling on breast and belly range from all white to largely black (Bédard, and Sealy 1984; Jones 1990). The back is dark-grey to black in all plumages but the scapulars have a variable number of white feathers in them, forming a white line on each side of the back. In its breeding environment a dark auklet appears cryptic but a white bird is conspicuous and stands out to a human observer from a distance.

We propose a new hypothesis for explaining the variation found in Least Auklet breeding plumage. The dark plumage camouflages the bearer from avian predators and thereby reduces its risk of being depredated during an ambush attack. Although physiologically cheaper to produce than a dark plumage (Veiga, and Puerta 1996), a white plumage should carry a cost in terms of increased predation risk because a conspicuous bird would be easier to detect on the ground. Since white birds are socially dominant and preferred in mate choice experiments (Jones 1990), we further hypothesise that the conspicuous white plumage is a strategic handicap that signals to aerial predators a strong flying performance and a low chance of capture.

From this hypothesis we make the following predictions:

1. Predators should prefer more cryptic prey if conspicuousness is a signal of unprofitability (Götmark, and Unger 1994).
2. If plumage is a strategic handicap, the degree of mottling should be an honest signal of flying performance and be negatively correlated with it.
3. In the absence of aerial predators, the physiologically cheaper plumage should be more common and plumage variation should be less since the cost of increased predation risk associated with bright plumages is removed.

This study took place on Buldir Island (52°21'N 175°56'E) in the western Aleutian Islands, Alaska. Auklets gather each morning on the talus surface throughout the breeding season from May to August (Byrd *et al.* 1983). Glaucous-winged Gulls (*Larus glaucescens*) and Peregrine Falcons (*Falco peregrinus*) are common and frequently hunt auklets. Buldir has no foxes or other land predators. The Pribilof Islands of St. Paul (57°07'N 170°16'W) and St. George (56°35'N, 169°40W) in the southeastern Bering Sea are 1200 km NE of Buldir. In contrast to Buldir, large gulls hardly ever visit auklet colonies on the Pribilof Islands and predation Snowy Owls (*Bubo scandiacus*) or Gyr Falcons (*Falco rusticolus*) is also very rare.

are virtually absent on the Pribilof Islands but predation by Arctic Foxes (*Alopex lagopus*) is not uncommon. We test our three predictions by 1. conducting a model predation experiment, 2. by measuring plumage pigmentation and take-off speed and 3. by comparing Least Auklet plumages between Buldir and the Pribilof Islands.

Methods

Model experiment

We experimentally manipulated the underside of realistic models to resemble the extremes of mottling found within the natural variation of Least Auklet plumage. We used Titanium-dioxide based acrylic paint and black Sharpie® felt pens for white and black, respectively. In contrast to mammals, birds can see in the near ultraviolet (UV) (Bowmaker 1980). UV reflectance is widespread among avian taxa (Eaton, and Lavon 2003); however, areas of high UV reflectance on plumage are generally iridescent (Andersson, and Amundsen 1997; Bennett *et al.* 1997; Andersson *et al.* 1998; Pearn *et al.* 2003). What appears white to the human eye has generally high UV reflectance and what appears black has almost always low reflectance in the UV spectrum (Eaton, and Lavon 2003). Since Least Auklets possess only black pigments and no structural, iridescent colours in their feathers, we had no reason to assume that either a painted or a natural auklet would look very different to a gull than to a human. We built the models from taxidermically prepared Least Auklets found dead on the talus to resemble as closely as possible a live auklet standing on the surface.

We presented models to gulls patrolling over the auklet colony on Main Talus, Buldir Island, during the morning activity period of the summers 2000 to 2002. Live auklets frequently gathered around the models. Models were always presented in pairs, a dark matched with a light model. We placed one or two pairs about ten meters from an observation blind so that they could be seen from every direction. A distance of at least

five meters was maintained between each model. While an attacking gull might detect the more conspicuous model first from a greater distance, it was likely to see the second model before initiating the final attack. At the beginning of each observation session we randomised the position of the models by coin-toss and kept the models under continuous watch for the time of the session (3 to 4 hours). After four weeks we repainted each model. To compensate for the potential that some models are more attractive to gulls than others, we changed the paint from white to black and visa versa every time the models were repainted. When gulls or Crested Auklets (*Aethia cristatella*) destroyed a model we replaced it. Since gulls did not receive any positive reinforcement when they caught a model auklet we presume that it is unlikely the same gull attacked the models disproportionately often.

Degree of plumage mottling

To measure the degree of mottling of Least Auklet plumages on Buldir Island we photographed each captured bird with a 100 mm f/2.8 macro lens on Aqua 100 ASA black-and-white film. A ring flash set to automatic exposure with the camera set to f/11 at 1/250s ensured consistent lighting. We held the birds by both wings in a standardised upright position with their body perpendicular to the camera axis (Figure 6.1). For analysis we scanned negatives on a Nikon Coolscan 4500 or an Epson 1680 at 1600 dpi. To compared plumage mottling of auklets from Buldir with those on the Pribilof Islands, we used 122 scans at 300 dpi of 9 cm × 13 cm photographic colour prints and 23 digital images (Nikon Coolpix 990, 3.3 megapixel) of adult Least Auklets in the hand captured on St. Paul from 1987 to 1989 (Jones 1990) and St. George in 2002 (H. Renner, unpubl.

data), respectively. We saved and archived all image files in jpeg format. After discarding colour information, where present, we analysed the images in ImageJ (Wayne Rasband, National Institute of Health, USA, available at http://rsb.info.nih.gov/ij/). We calibrated the exposure and contrast of each image from Buldir against a card containing a range of grey values held beside the bird (Figure 6.1) to ensure consistent measurements. To quantify mottling we measured average grey values of the images over the areas representing neck, chest, vent, and undertail (Figure 6.1) (terminology following Mullarney *et al.* 1999). We needed an alternative way of assessing plumage because the images on the Pribilof Islands were taken without a grey card for reference. Instead we visually scored the photographs on a scale from one to eight by comparing them with drawings of typical plumage stages (Figure 6.2). Each photograph was scored independently by five people. Mean visual plumage scores were closely related to mean grey values ($r^2 = 0.47$, Figure 6.3).

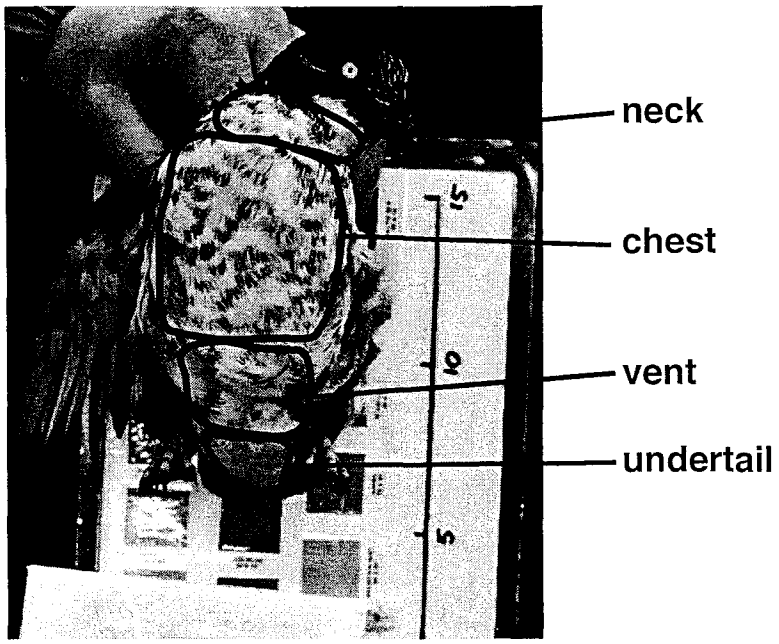


Figure 6.1 Quantification of plumage mottling. Mottling of four ventral plumage areas was measured as average grey-scale values from calibrated photos.

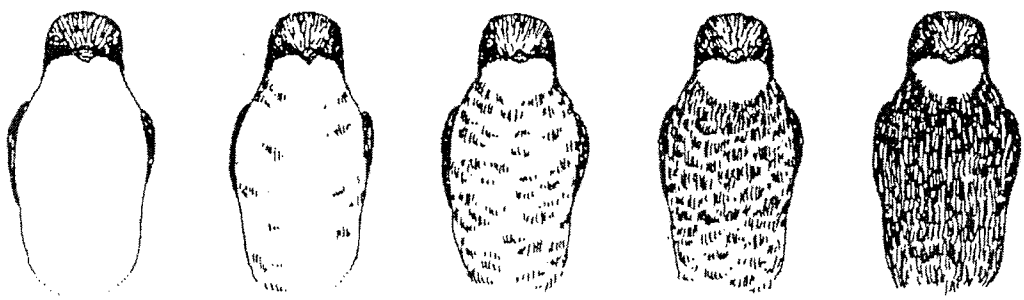


Figure 6.2 To compare photographs between islands (which involved uncalibrated photos), five independent observers estimated mottling on a scale of one to eight. Observers were instructed to select between which two drawings the bird's plumage fell, and which of these two drawings was the closest match. E.g., score 3 would indicate that the photo fell between the 2nd and 3rd drawing from the left, and was closer to the second.

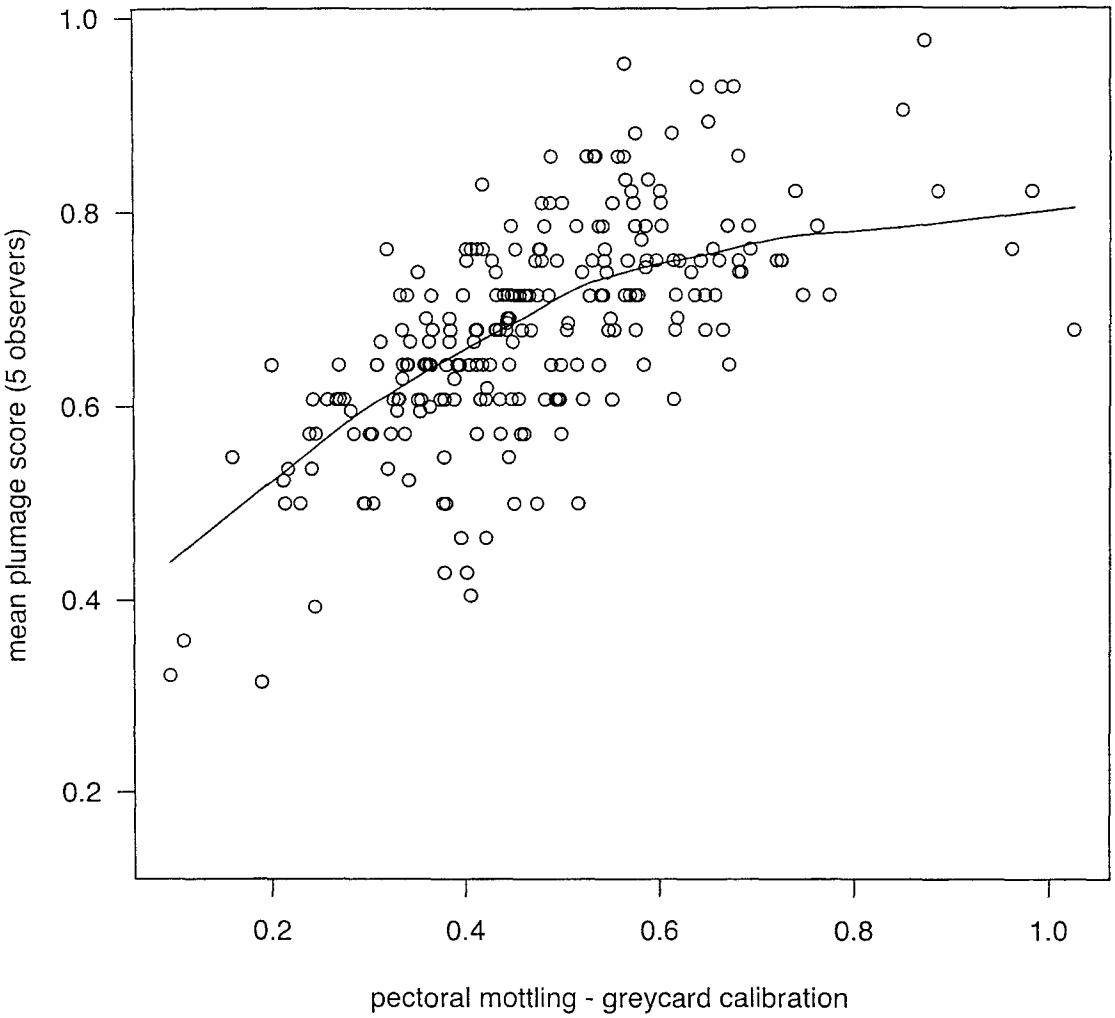


Figure 6.3 Relationship between two scales used to measure plumage mottling (as illustrated in Figure 6.1) of adult Least Auklets (*Aethia pusilla*) from Buldir Island. The line represents a lowess smoother showing a close link between both measures over much of the range. For particularly dark birds, the link between both methods was weaker.

Take-off acceleration

In a controlled take-off experiment, acceleration (adjusted for slope) at 0.17 seconds after losing contact with the substrate is a measure repeatable (72 %) across consecutive trials on the same individual (see Chapter 4). We chose this measure because it had the highest repeatability of all measures considered, and it is of direct relevance to flying performance and the potential outcome of a chase. We calculated acceleration from smoothed time-location data derived from digital video (see Chapter 4 for details).

Statistical analysis

We compared the total number of attacks on dark models with the number of attacks on white models with a binomial test. To test for a relationship between plumage mottling and take-off acceleration we used multiple linear regression. The sine of the downwards sloping trajectory was included to compensate for the slope-dependent gravity component to acceleration along the trajectory. For some birds we had multiple measurements of take-off acceleration within a season and over several seasons. Including several measurements for an individual bird would lead to an underestimate of the error variance (a.k.a. "pseudoreplication"). To avoid this problem, and lacking a balanced design, we used the data from any individual only from the year for which we had the most measurements. Within a year and individual we used the average take-off acceleration because there was no evidence of a trend within a season. We used R 2.0.1 (Ihaka, and Gentleman 1996; R Development Core Team 2004) for calculations of all statistics. We report means with their standard error.

Results

Predation experiment

At any one time five to ten mostly adult Glaucous-winged Gulls patrolled the talus hunting for auklets. Most actual auklet attacks happened so fast that it was difficult or impossible to observe details. During attacks, gulls plummeted downhill flying close over the ground. Auklets usually were caught in air, either immediately after being flushed from the ground or after a high-speed pursuit up to 100 m down the talus slope. When the auklet reached the water it often attempted to escape by diving underwater. The gull then hovered closely above the surface and followed the diving auklet, attempting to catch it when the auklet resurfaced. Captured Least Auklets were generally swallowed whole.

Attacks observed on model auklets were similar to natural predation events. Gulls approached in flight and usually grabbed the model auklet by the head without landing. One observation in which a gull walked toward a model was excluded from the sample. During three breeding seasons we recorded 28 gull attacks on model Least Auklets, all by adult gulls. Glaucous-winged Gulls attacked dark models significantly more often than white models (20 attacks on dark, 8 attacks on white models, binomial test, $P = 0.036$, Figure 6.4).

Plumage comparison between islands

Least Auklets breeding on the gull-free Pribilof Islands were significantly less mottled than Least Auklets from Buldir (Figure 6.5, $t = -39.7$, $df = 428$, $P < 0.001$). All

five observers scored in the same direction and confirms the impressions held by several researchers familiar with auklets on both islands (F. M. Hunter, I. L. Jones, N. B. Konyukhov, H. M. Renner, pers. comm.; pers. obs.). No differences in mottling were detected between the two Pribilof Islands ($t = -1.15$, $df = 139.9$, $P = 0.25$). While the full range of plumage mottling is not found in the sample from each island, birds of covering the full range of mottling can be found in each of these colonies. Variance does not differ between the birds from Buldir and those from the Pribilof Islands (Levene's test, $F = 2.35$, $df = 1, 428$, $P = 0.13$).

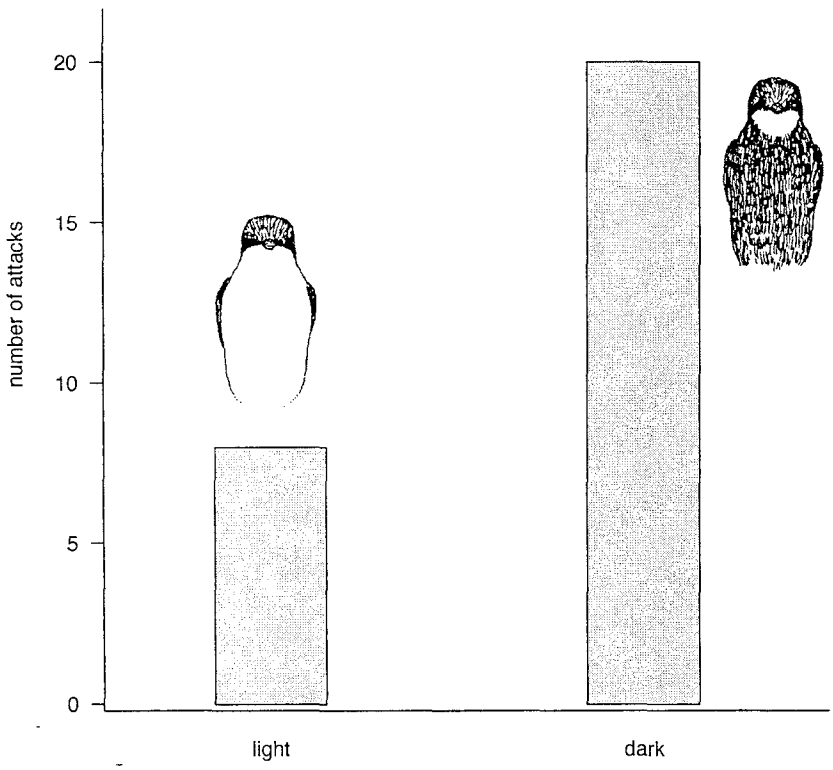


Figure 6.4 Glaucous-winged Gull (*Larus glaucescens*) attacks recorded on Least Auklet (*Aethia pusilla*) models painted black and white, respectively and presented in pairs. Dark models were attacked significantly more frequently than light models (binomial test, $P < 0.05$)

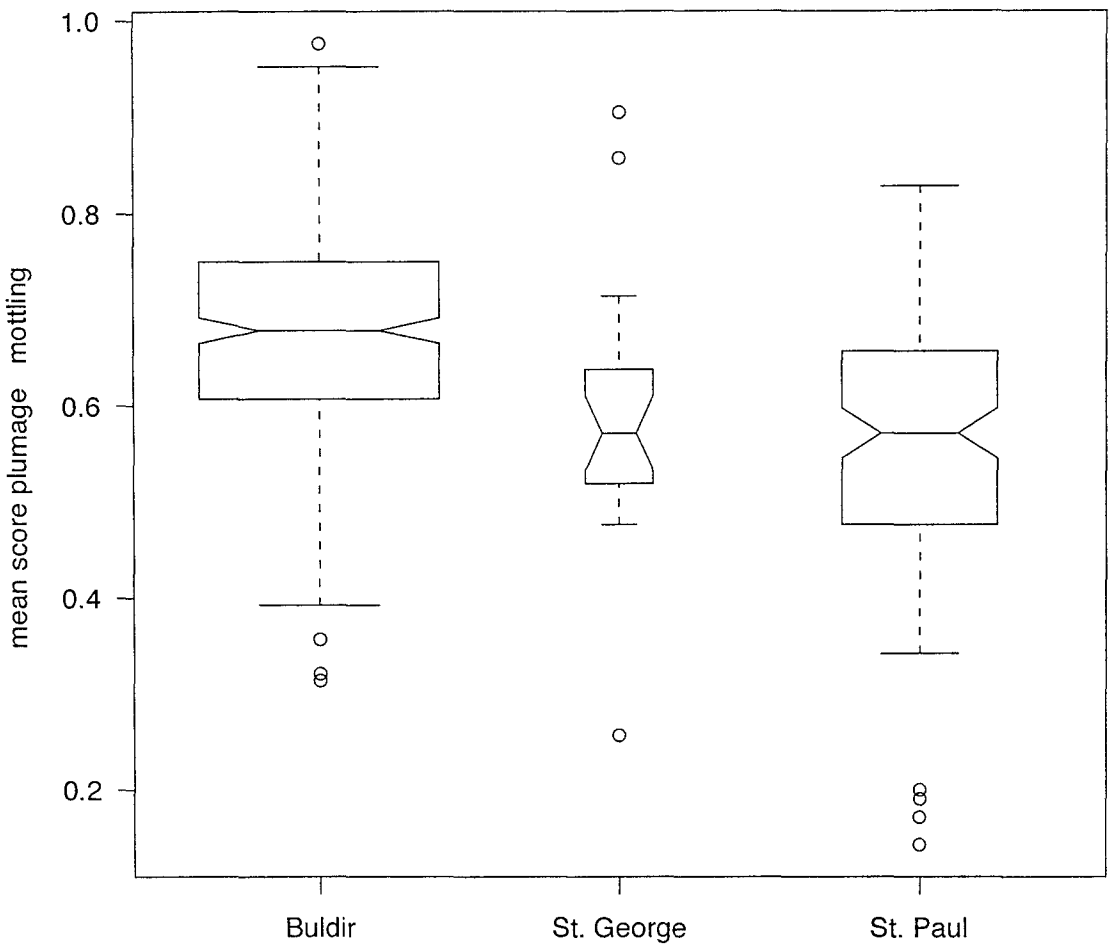


Figure 6.5 Comparison of plumage mottling of adult Least Auklets (*Aethia pusilla*) between Buldir Island, where gull predation is common and St. George and St. Paul (Pribilof Islands) where gull predation is absent. Birds from Buldir are significantly darker than birds from the Pribilof Islands.

Plumage mottling and take-off acceleration

Contrary to our prediction, we did not find a negative relationship between plumage mottling and take-off acceleration (Table 6.1). Once a single outlier that slipped during take-off is removed, the relationship between neck and take-off acceleration disappears, too ($t = 1.37$, $df = 121$, $P = 0.17$).

Table 6.1 Linear model of comparing the degree of mottling of different plumage sections of Least Auklets (*Aethia pusilla*) from Buldir Island to log take-off acceleration (0.17 s after take-off).

	Estimate	SE	t	P
(Intercept)	1.191004	0.062808	18.963	< 0.001 ***
neck	0.117292	0.047822	2.453	0.0152 *
pectoral	0.210471	0.141362	-1.489	0.1384
vent	0.094694	0.11839	0.8	0.4249
undertail	0.040348	0.056387	0.716	0.4752
white scapulas [1)]	0.002148	0.002809	0.765	0.4455

[1)] In contrasts to the other plumage measurements, high values represent lighter birds here

Discussion

This is the first study to examine predator preference for a plumage trait, experimentally manipulated within a species' natural range of variation. We found Glaucous-winged Gulls preferentially attacked dark models of Least Auklets. This observation matches the prediction of the handicap model between predator and prey, assuming that plumage is indicative of unprofitable prey.

A study with experimentally manipulated models of Australian lizards found that birds of prey attacked the conspicuous model more frequently (Stuart-Fox *et al.* 2003). In that case, conspicuousness could be a handicapped signal in social interactions of the lizard, but not in predator-prey interactions. In a series of papers Götmark tested the frequency with which European Sparrowhawks (*Accipiter nisus*) attacked natural models of different species or sex (Götmark 1992, 1993; Götmark, and Unger 1994). None of these models was experimentally manipulated, however, but selected based on their natural differences in conspicuousness. The study was therefore unable to distinguish between a predator's preference for conspicuousness and a pre-existing preference for a particular sex or species. Results varied widely – in Chaffinch (*Fringilla coelebs*), attacks on conspicuous male models were more common, whereas in Pied Flycatcher (*Ficedula hypoleuca*), dull female models were attacked more often (Götmark 1993). Experiments with experimentally manipulated models could show whether the observed preference of an avian predator for the less conspicuous prey item is a more widespread phenomenon. So far, this kind of predator-prey communication has received little attention.

Warning or aposematic colouration is widespread in many taxa, especially insects. The case for aposematic colouration as an indicator of unpalatability (Huxley 1938) has mainly been made for the Hooded Pitohui (*Pitohui dichrous*) and is generally thought to be an exception among birds (Diamond 1992; Dumbacher *et al.* 1992; Mouritsen, and Madsen 1994). Rather than selecting dark Least Auklets, it is also possible that Glaucous-winged Gulls confused models of dark Least Auklets for Crested Auklets (*Aethia cristatella*). Crested Auklets are more common on Buldir and represent a substantially larger meal (about 260 g total mass compared to 85 g in the average Least Auklet). However, apart from the different ornaments and shape, the large size difference is very apparent to the human eye in the field, even when the two species are not seen side by side. We consider it unlikely that gulls, which hunt auklets for a living, would be unable to distinguish the species by shape and size alone.

It has also been suggested that plumage polymorphism could evolve in a prey species to avoid a predator's search image (avoidance-image hypothesis) for the more common morph (Paulson 1972; Rohwer 1983; Rohwer, and Paulson 1987). It has been argued that this mechanism is the most common evolutionary cause of polymorphisms in birds (Galeotti, and Rubolini 2004). For two reasons the kind of polymorphism found in the mottling of the underside of Least Auklets does not fit this hypothesis. First, polymorphisms are generally not found in the prey of intelligent predators but rather in the predators of prey organisms of low intelligence (Galeotti, and Rubolini 2004). Least Auklet themselves do not pursue intelligent prey, however. The avoidance-image hypothesis is nevertheless an unlikely explanation for plumage variation in Least Auklets

because, in the continuous gradation of plumage mottling, the intermediate forms are the most common (Figure 6.5).

If gull predation is the cost that turns a white alternate plumage into a handicap, we predicted that the average plumage is darker in the presence of gulls than in their absence. We found this effect in a natural experiment by comparing Least Auklets from Buldir Island with those from the Pribilof Islands where gull predation is rare, again supporting the handicap model.

We presumed that dark birds are easier to capture because they are on average subordinate in social interactions and possibly younger (Jones 1990). These birds might therefore be less experienced and capable of escaping an attack. Measurements of take-off acceleration by captured Least Auklets on release do not support the idea that dark birds are weaker fliers. There is some evidence that Least Auklets become less mottled with age (Jones, and Montgomerie 1992). While older, more experienced birds might not have a higher flying speed, they might be better at executing the turning gambit (Howland 1974; Hedenström, and Rosén 2001), initiating a tight turn at the optimal distance to evade a pursuing predator. In Feral Pigeons (*Columba livia*) there is evidence that melanistic forms are weaker fliers than other morphs (Johnston, and Janiga 1995, p. 160). More data are needed on the relationship of pigmentation and flying performance, and on the plumage of Least Auklets actually taken by gulls.

While extensively explored on theoretical grounds, there are still few empirical data demonstrating that the handicap principle works, especially in predator prey interactions. Most of our results are consistent with the light alternate plumage of Least Auklets being

a handicap when interacting with Glaucous-winged Gulls. We did not find a confirmation, however, that plumage mottling is related to flying performance during take-off.

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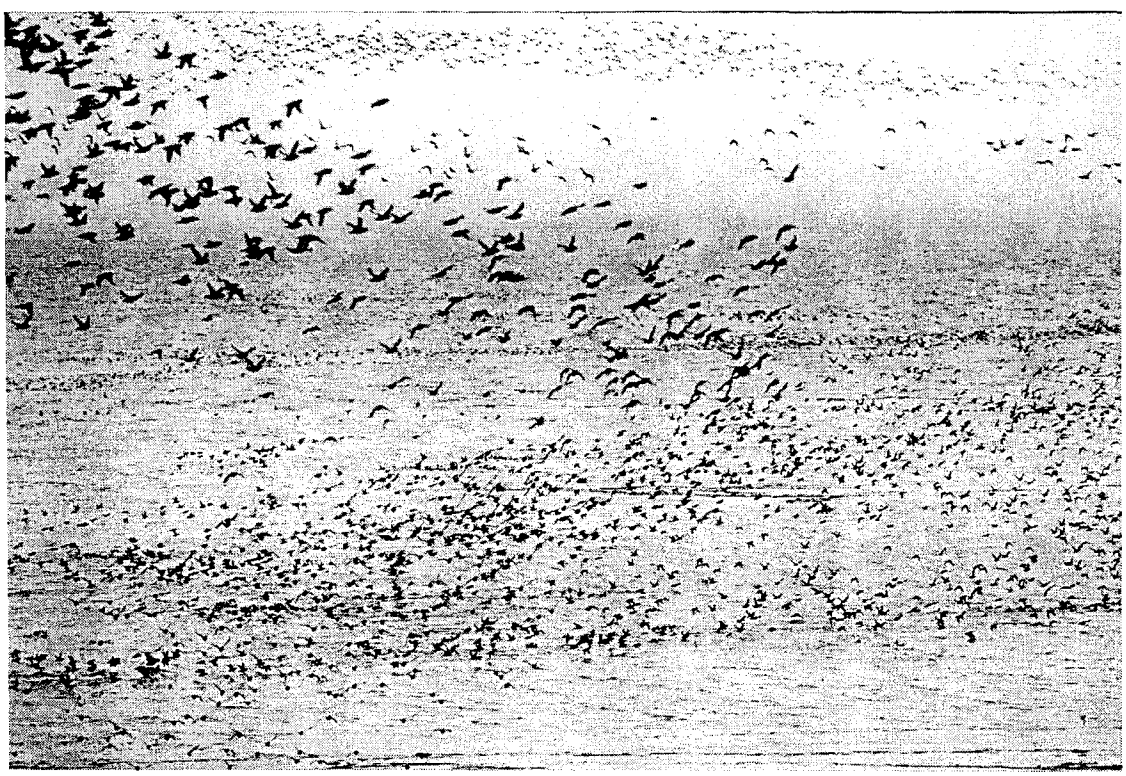
Chapter 7.

Summary



I set out to examine the evolution of plumage and ornament variation in Least Auklets *Aethia pusilla* on Buldir Island. Prior studies had shown that there was a mating preference for long auricular plumes (Jones, and Montgomerie 1992), and that plumage mottledness was related to social dominance and assortative mating (Jones, and Montgomerie 1991).

To set the scene, I examined the evolution of pigmentation, in particular of the tuxedo pattern, in seabirds. I found evidence that social selection plays a role in the evolution of seabird pigmentation. I also investigated the breeding biology of Least Auklets on Buldir Island. Least Auklets on Buldir reached a lower fledging mass than those on St. George Island, indicating that food was more readily available at the latter site.

Some models of communication demand that there has to be a cost associated with a signal, if it is to convey a reliable message. In the case of the relatively small ornaments displayed by Least Auklets (in comparison to the ornaments displayed by some polygynous species, for example) and especially in the case of the ventral plumage mottling, it is unclear what this cost could be. There are numerous examples of plumage pigments being related to measures of individual quality or status (Rohwer 1975; McGraw *et al.* 2003; Safran, and McGraw 2004), and the production of plumage pigments has been shown to be energetically costly (Hill 2000). By contrast, in the case of Least Auklets, I found that a lack of pigment (and conspicuousness) is positively related to a measure of quality (mass).

I tested the hypothesis that the more conspicuous white plumage is a handicap in auklets' interactions with predatory Glaucous-winged Gulls (*Larus glaucescens*). This handicap could be the cost that maintains honesty in the social system as well. If conspicuousness would be the only factor in auklet-gull interactions, we would expect gulls to attack white birds more frequently. However, it would then be difficult to explain why all Least Auklets are not ventrally dark (like Crested Auklets (*A. cristatella*), for example). I found that gulls attacked experimentally darkened models significantly more frequently than lightened models. This result is consistent with white plumage being a vulerability handicap (see Vehrencamp 2000). However, I did not find the expected link between plumage and take-off performance. It is possible that the variable I measured (acceleration) was not the most crucial in surviving a gull attack, especially since melanistic pigeons are weaker fliers than other morphs (Johnston, and Janiga 1995 p. 160).

Body mass is probably the most widespread measurement taken on wild birds and is often taken as a proxy for some other, less tangible quality, like viability or even evolutionary fitness. The most fundamental factor affecting body mass is food availability; a starving bird will lose mass. Especially in seabirds, body mass is often seen as a direct indicator of food availability, nutritional density of the diet, or foraging ability. This has to hold true when food is scarce, but would not be expected for a bird feeding *ad libitum* (Figure 7.1). Consequently, if I postulate a relationship between a measure of individual quality, such as foraging ability, and body mass, we might only find this relationship when food is scarce. However, an increased risk of predation can also lead to

a decrease in body mass, because a bird of lower mass is more manoeuvrable and therefore more likely to escape an aerial predator (Gosler *et al.* 1995). While Glaucous-winged Gulls and Peregrine Falcons (*Falco peregrinus*) are common on Buldir Island, auklets nesting on the Pribilof Islands are remarkably free of avian predation. Both differences in food availability and differences in predation pressure can therefore lead to differences in adult body mass. A comparison between chick growth data, however, suggests that prey are indeed more readily available or of a higher quality on the Pribilof Islands (Roby, and Brink 1986) than on Buldir Island (Chapter 3). Lower food availability would have increased my chance of detecting relationships between quality indicators and plumage or ornaments compared to the study on the Pribilof Islands (Jones, and Montgomerie 1992).

My study indicates that even small ornaments with apparently only small physiological costs can have significant, but often complex relationships with indicators of physical fitness. The possibility that sexual selection interacts with predator-prey relationships is an important consideration that should be taken into account in future studies.

Figure 7.1 Conceptual relationship between food availability and body mass

Future research needs

I had to make the assumption that take-off acceleration is directly related to a bird's likelihood to survive a gull attack and therefore is useful as an indicator of individual quality. It would be instructive to test this assumption. This could be done by measuring take-off behaviour of a fairly large sample of birds, which are then followed over several years to estimate survival. To conduct such a study, it would be advisable to first develop a system that could record time-location data from video automatically. This could be accomplished by conducting the take-off experiment in front of a neutral background and scripting existing software. Experimental manipulations of food availability could help determine the nature of any relationship between take-off performance and body mass.

Least Auklets are unique, to my knowledge, in that there is a negative rather than positive relationship between pigmentation and indicators of quality. In other birds,

deposition of melanin is related to levels of testosterone during moult (Evans *et al.* 2000). It appears that this mechanism is reversed in Least Auklets. Therefore it would be interesting to study the link between endocrinology and plumage expression in this species.

Least Auklets are great study subjects because they are abundant, easy to catch, have complex behaviours, an extended courtship period, and live in cool places. Fortunately for those of us that love working with them, there is still much to learn.

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